CANADIAN THESES ON MICROFICHE

THÈSES CANADIENNES SUR MICROFICHE

National Library of Canada
Collections Development Branch

Canada Theses on
Microfiche Service

Ottawa, Canada
K1A 0N4

Bibliothèque nationale du Canada
Direction du développement des collections

Service des thèses canadiennes
sur microfiche

NOTICE

The quality of this microfiche is heavily dependent upon the quality of the original thesis submitted for microfilming. Every effort has been made to ensure the highest quality of reproduction possible.

If pages are missing, contact the university which granted the degree.

Some pages may have indistinct print especially if the original pages were typed with a poor typewriter ribbon or if the university sent us an inferior photocopy.

Previously copyrighted materials (journal articles, published tests, etc.) are not filmed.

Reproduction in full or in part of this film is governed by the Canadian Copyright Act, R.S.C. 1970, c. C-30. Please read the authorization forms which accompany this thesis.

AVIS

La qualité de cette microfiche dépend grandement de la qualité de la thèse soumise au microfilmage. Nous avons tout fait pour assurer une qualité supérieure de reproduction.

S'il manque des pages, veuillez communiquer avec l'université qui a conféré le grade.

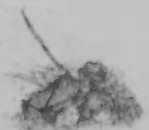
La qualité d'impression de certaines pages peut laisser à désirer, surtout si les pages originales ont été dactylographiées à l'aide d'un ruban usé ou si l'université nous a fait parvenir une photocopie de qualité inférieure.

Les documents qui font déjà l'objet d'un droit d'auteur (articles de revue, examens publiés, etc.) ne sont pas microfilmés.

La reproduction, même partielle, de ce microfilm est soumise à la Loi canadienne sur le droit d'auteur, SRC 1970, c. C-30. Veuillez prendre connaissance des formules d'autorisation qui accompagnent cette thèse.

THIS DISSERTATION
HAS BEEN MICROFILMED
EXACTLY AS RECEIVED

LA THÈSE A ÉTÉ
MICROFILMÉE TELLE QUE
NOUS L'AVONS REÇUE



Canada

CIHM / ICMH

National Library of Canada
Bibliothèque nationale du Canada

Canadian Theses on Microfiche Service
Service des thèses canadiennes sur microfiche

NL-91 (4/77)

PERMISSION TO MICROFILM — AUTORISATION DE MICROFILMER

Please print or type — Écrire en lettres moulées ou dactylographier

AUTHOR — AUTEUR

Full Name of Author — Nom complet de l'auteur

Michael Bruce Bakalo

Date of Birth — Date de naissance

Feb 11 1956

Country of Birth — Lieu de naissance

Canada

Permanent Address — Résidence fixe

1806 Ghostpine Dr.
Fort McMurray, Alta T9H 3Z8

THESIS — THÈSE

Title of Thesis — Titre de la thèse

Host Selection by the Arctic Species

Degree for which thesis was presented — Grade pour lequel cette thèse fut présentée

M. Sc.

Year this degree conferred — Année d'obtention de ce grade

1985

University — Université

University of Alberta

Name of Supervisor — Nom du directeur de thèse

John F. Addison

AUTHORIZATION — AUTORISATION

Permission is hereby granted to the NATIONAL LIBRARY OF CANADA to microfilm this thesis and to lend or sell copies of the film.

The author reserves other publication rights, and neither the thesis nor extensive extracts from it may be printed or otherwise reproduced without the author's written permission.

L'autorisation est, par la présente, accordée à la BIBLIOTHÈQUE NATIONALE DU CANADA de microfilmer cette thèse et de prêter ou de vendre des exemplaires du film.

L'auteur se réserve les autres droits de publication; ni la thèse ni de longs extraits de celle-ci ne doivent être imprimés ou autrement reproduits sans l'autorisation écrite de l'auteur.

ATTACH FORM TO THESIS — VEUILLEZ JOINDRE CE FORMULAIRE À LA THÈSE

Signature

Michael Bakalo

Date

March 21, 1985

Canada

THE UNIVERSITY OF ALBERTA

HOST SELECTION BY TWO APHID SPECIES

BY

Michael L. Roelofs

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE

OF Master of Science

Department of Zoology

EDMONTON, ALBERTA

Spring 1985

THE UNIVERSITY OF ALBERTA

RELEASE FORM

NAME OF AUTHOR Michael P. Antolin

TITLE OF THESIS HOST SELECTION BY TWO APHID SPECIES

DEGREE FOR WHICH THESIS WAS PRESENTED Master of Science

YEAR THIS DEGREE GRANTED Spring 1985

Permission is hereby granted to THE UNIVERSITY OF ALBERTA LIBRARY to reproduce single copies of this thesis and to lend or sell such copies for private, scholarly or scientific research purposes only.

The author reserves other publication rights, and neither the thesis nor extensive extracts from it may be printed or otherwise reproduced without the author's written permission.

(SIGNED) Michael Antolin

PERMANENT ADDRESS:

[redacted]

DATED March 21 1985

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled HOST SELECTION BY TWO APHID SPECIES submitted by Michael P. Antolin in partial fulfilment of the requirements for the degree of Master of Science.

.....
Supervisor

.....

.....

.....

Date. March 21, 1985

Dedication

This thesis is dedicated to the memory of my father, Victor Antolin, who passed away on his sixty-second birthday on July 1, 1984. His enthusiastic appreciation of Nature, and especially plants, sparked my interest in biology; his encouragement led me to pursue biology as a profession. In his humility, he proved himself a man capable of abiding and understanding Life, from the grand to the prosaic. I can only hope to emulate him by carrying that legacy with me.

Abstract

This thesis describes an experimental study of the patterns of habitat (host plant) selection by *Macrosiphum valeriani* (Clarke) and *Aphis varians* Koch, two aphid species that feed on the inflorescence of fireweed (*Epilobium* (=*Chamerion*) *angustifolium* L.). I examined the effects of fireweed quality, inter- and intraspecific aphid densities, ant attendance and predators on aphid host selection and distributions. Experiments encompassed a number of spatial scales over which aphids may choose fireweed: areas, plots within areas, and shoots within plots.

Both species selected the largest fireweed shoots (those shoots that provide the highest population growth rates), but the spatial scales of fireweed choice differed between the two species. *Macrosiphum valeriani* selected large fireweed shoots within areas of tall fireweed. Although *A. varians* did not discriminate among areas of fireweed, they were found on the largest shoots within areas. These aphid species have the potential to compete for resources on fireweed shoots, and competition between these species affects their performance. Neither species, however, reacted to inter- or intraspecific aphid densities. *Aphis varians* has a mutalistic relationship with ants, yet *A. varians* colonists did not positively associate with ants. *Macrosiphum valeriani* did not discriminate among areas with ants or without ants, nor was *M. valeriani* directly affected by ants. Predators and parasitoids responded quickly to

increasing densities of both aphid species, and had significant impacts on aphid population growth and survival.

These results, together with results from other studies in this system (Addicott 1978, 1979), suggest that the differences in host selection by *M. valeriani* and *A. varians* represent two strategies for minimizing the impacts of predators. These strategies are linked to the life histories and dispersal abilities of the aphids. *Aphis varians* selects tall fireweed that maximize population growth, offspring populations quickly attain density high enough for the production of winged migrants, and some of those migrants survive to disperse to other fireweed. *Aphis varians* minimizes predator impacts by satiating predators, by escaping predators in time by flying to other areas and by associating with ants. *Macrosiphum valeriani* selects areas of tall fireweed. Instead of dispersing only by winged migrants, it also disperses as apterae to fireweed shoots within the area chosen by initial colonists. In this case, *M. valeriani* avoids predators by moving off fireweed shoots under predator attack.

These results are briefly cast in the light of habitat selection theory. Theories of habitat selection are based primarily on the relationship between intrinsic habitat quality and the density of residents within a habitat, and how that relationship affects habitat choices that colonists face. Theoretical studies conclude that competition is the driving force determining how organisms choose habitats.

Habitat selection theory falls short in describing host selection by *M. valeriani* and *A. varians* because competition is not a strong factor influencing host selection of either aphid species. First, the relationship between intrinsic habitat quality and resident density is not predictable because of the relatively low survival of colonists and resident populations. Second, differences in life history and scales of habitat selection by *M. valeriani* and *A. varians* diminish the probability of successful populations of both species co-occurring on the same fireweed shoot.

Acknowledgements

None of this would have been possible without the perseverence and support of John F. Addicott, whose initial work with the aphid-ant-fireweed system provided the impetus for this study. Too many people to list individually, both at the University of Alberta and the Rocky Mountain Biological Laboratory, contributed in some way. Maintaining sanity is an important aspect of any thesis, and I would like to thank all those who played hockey (especially Mike Schroeder and the old can game), Dirk Van Vuren, Pat Carter and the other denizens of the nefarious Red Rocks Delta and the impeccable Ghetto at R.M.B.L., Parks Canada, Jasper National Park and Sick's Lethbridge Brewery. Financial support was provided by the Department of Zoology, University of Alberta, NSERC operating grants to J.F.A, and a Sigma Xi Grant-in-Aid of Research to M.F.A.

Table of Contents

Chapter — Page

I. Introduction 1

A. Models of habitat selection 2

B. Spatial scales -- what is a habitat? 6

C. Literature Cited 8

II. Determinants of distributions in two co-occurring aphid species: habitat selection and spatial scales 10

A. Introduction 10

Biology of the aphid system 11

B. Study sites and methods 15

1982 experiment 16

1983 experiment 19

C. Results 21

1982 experiment 21

Spatial scales and host plant effects 21

Areas 23

Plots 26

Individual fireweed shoots 31

Effects of aphids 36

Effects of ants 43

1983 experiment -- effects of predators 45

D. Discussion 48

The role of competition 50

The roles of ants and predators 52

The effects of pheromones 54

Conclusions 55

E. Acknowledgements 57

F. Literature cited 59

III. The effects of aphid density on the host selection and colony survival of *Macrosiphum valeriani* Clarke (Homoptera: Aphididae) 64

A. Introduction 64

B. Materials and methods 67

Colonization experiments 67

Survival and reproduction experiments 70

C. Results 71

Colonization 71

Survival and reproduction 80

D. Discussion 87

Fireweed quality 88

Interference by other insects 89

Comparison of apterae and alates 92

Conclusions 93

E. Acknowlegements 96

F. Literature cited 97

List of Tables

Table		Page
1	Two-way nested analysis of variance of fireweed shoot height at Coal Creek, 1982	22
2	The numbers of fireweed shoots (plots), shoots colonized, and numbers of aphids colonizing per shoot in the five areas at Coal Creek in 1982	25
3	Rank correlation coefficients between plot characteristics and the numbers of aphids colonizing plots at Coal Creek in 1982	30
4	Types of colonizations on shoots from removal plots, and on shoots from four categories of marking plots at Coal Creek in 1982	41
5	Interspecific and intraspecific correlations between numbers of aphid colonists and resident density at Coal Creek in 1982	42
6	Comparison of numbers of plants colonized by *M. valeriani* among treatments in 1983 screenhouse experiments	72
7	Median numbers of *M. valeriani* found on colonized plants in 1983 screenhouse experiments	74
8	Rank correlation coefficients between numbers of *M. valeriani* colonists, resident density and fireweed height in 1983 screenhouse experiments	75
9	Slopes and r^2 values of the regression between log(x+1) number of colonizing *M. valeriani* and average distance from release points in 1983 screenhouse experiments	77

10 Mean numbers of [illegible] seedlings found in survival experiment at Spring Creek, 1984.....81

11 Numbers of fireweed shoots, average fireweed shoot height, and fates of adult *M. valeriani* at Spring Creek, 1984.....82

12 Reproduction by *M. valeriani* in survival experiment at Spring Creek, 1984.....83

List of Figures

Figure | Page

1 Areas and plots of A.) 1982 colonization experiment, and B.) 1983 predation experiment.....17

2 Distribution of colonization by *M. valeriani* and *A. varians* at each sampling period during the 1982 experiment.....24

3a Comparison between distributions of aphids colonizing plots in the 1982 colonization experiment and distributions expected from random colonization model. Removal plots.....28

3b Comparison between distributions of aphids colonizing plots in the 1982 colonization experiment and distributions expected from random colonization model. Marking plots.....29

4 Comparison between distributions of numbers of recolonizations of fireweed shoots in the 1982 experiment and the expected distribution generated from a model of random colonization.....32

5 Comparison between distributions of types of colonizations of fireweed shoots in the 1982 colonization experiment and the expected distributions generated from a model of random colonization.....33

6 Distributions of the heights of colonized and uncolonized fireweed shoots in 1982.....35

7 Interaction between fireweed shoot height, shoot exposure, and probability of colonization on individual fireweed shoots in 1982.....37

8 Comparison between treatments of the numbers of

sampling periods in which individual fireweed shoots were colonised in the 1982 colonisation experiment....39

9 Response to the presence of ants by both aphid species in the 1982 colonisation experiment.....44

10 Predator's response to aphids in the 1983 Coal Creek experiment.....46

11 Relationship between colonisation by alate *M. valeriani* and fireweed height in 1983 screenhouse experiment.....79

12 Relationship between number of *M. valeriani* remaining on a fireweed shoot and the size of the *A. varians* colony on the shoot, 1984 Spring Creek experiments 83

13 Correlation between the size of the developing *M. valeriani* colony and the size of the *A. varians* colony on a fireweed shoot, 1984 Spring Creek experiments 86

Introduction

Habitat selection is one of the most important factors determining the distributions of organisms (Elton 1966, Andrewartha and Birch 1954). Over the last fifty years, ecologists have documented that

> ...most animals are, in practice, limited in their distribution by their habits and reactions, the latter being so adjusted that they choose places to live in, which are suitable to their particular physiological requirements or to their breeding habits (Elton 1966, p. 40).

Generally, habitat selection is a behavioral phenomenon, that can be as simple as a taxis (e.g. blowfly larvae avoiding light), or part of complex behavioral interactions (e.g. the maintainence of territories by breeding birds: Fretwell 1972, Fretwell and Lucas 1970, Cody 1981). Studies of habitat selection have been carried out on organisms ranging from planthoppers (Denno et al. 1980) to birds (Lack 1933, 1937). The majority of this work was descriptive. Most investigations showed behavioral or physiological adaptations and constraints on habitat selection that may account for animal distributions [for example see the treatment of the topic in Krebs (1978)]. Much of the recent work on habitat selection has been directed toward discovering mechanisms promoting coexistence between competitors (both interspecific and intraspecific; Hallet 1982, Rosenzwieg 1973, Whitham 1980).

The objective of this research was to examine experimentally the role of habitat (i.e. host plant) selection in determining the distributions of two aphid species, *Macrosiphum valeriani* (Clarke) and *Aphis varians* Koch (Homoptera: Aphididae). Both species feed on the inflorescence of the same summer host, fireweed (*Epilobium* (=*Chaemerion*) *angustifolium* L.: Onagraceae). This system was chosen for two reasons. First, these two species are potential competitors, so that interspecific aphid interactions may affect host selection. Experimental work on the relationship between habitat selection and interspecific competition is practically nonexistent. Second, most work on habitat selection has been developed around a framework of density-dependent population regulation within habitats and the dominance of intraspecific competition in organizing single species distributions among habitats. Experimental work on a two-species system could lead to an extension of habitat selection theory.

A. Models of habitat selection

The theory of habitat selection predicts that organisms will place themselves in habitats where they maximize their fitness. Habitat selection models assume organisms are able to assess the quality of the habitats they sample and then select the ones in which fitness will be highest (the ones that are most "suitable"). The models can be separated into two types: those explaining the distribution of single

species (Fretwell 1972, Doyle 1975) and those exploring mechanisms of species coexistence (MacArthur and Levins 1964, Rosenzweig 1974,1981).

Of the single species models, Fretwell's (1972) has received the most attention. Fretwell, working with birds, assumed that some habitats are consistently selected over others, as opposed to all habitats being selected according to their abundances. He built his model around an 'ideal free distribution' of colonizations. This distribution was 'ideal' because organisms were assumed to select the habitat that would without exception maximize fitness; it was 'free' because all colonists were assumed to have an equal probability of gaining a suitable habitat, whether they were the 1st, 2nd, or nth colonizer. A colonist's assessment of a habitat, however, depended on the density of other birds within that habitat, and a colonist's fitness varied inversely with resident population density because resources were divided among more individuals. This model was used to give greater understanding of the function of territories in population biology.

Whitham (1980) verified this model for *Pemphigus* aphids on narrowleaf cottonwood, by demonstrating the importance of intraspecific competition in the aphids' habitat selection. He found that after long territorial bouts (Whitham 1979), the aphids galling larger leaves had greater average fecundity and survival than those on small leaves, and that position of the gall on the leaf was important as well.

The second single species model (Doyle 1975) was developed for the polychaete worm *Spirorbis borealis* to test whether its selection was coarse-grained or fine-grained. Doyle's model had no density dependence. His model was a Markov process, and included probabilities of individual larvae encountering different substrates, and their probabilities of settlement, metamorphosis and survival. The model explored how animals select in a heterogeneous mix of two habitats (i.e. *Fucus* species), and predicted that the worms would be highly selective (selection would be coarse grained) if early survivorship of individual larvae was high. Doyle also examined the effects of time. He found that *Spirorbis* larvae were less selective through time, that their behavior changed from selective to non-selective as time spent searching for suitable habitats increased.

Theoretical studies that model habitat selection as a mechanism promoting species co-existience use habitat preference as a niche parameter separating competing species (MacArthur and Levins 1964). MacArthur and Levins predicted that within the same environment, habitat choice must be coarse grained for specialist species to coexist. Otherwise one species, the superior competitor, would displace the other less competitive species. Rosenzweig (1973, 1981) followed this approach in a number of models and in a test using heteromyid rodents (Rosenzweig 1973). In a series of field experiments, he found that the habitat preferences of a kangaroo rat and a pocket mouse differed considerably, and

that the differences were crucial to their coexistence. Hallett (1982) has similar results for desert rodents. The critical assumption underlying these studies was that competitive effects among species would eventually lead to the evolution of habitat specialization, and therefore differences in habitat preference.

Many of the assumptions of the models discussed above are valid for the aphid-fireweed system. Pretwell's (1972) model revolved about resources not being monopolized by one or a few individuals; fireweed aphids are not despotic, so that the assumption of a 'free' distribution is met. Doyle's (1975) model is appropriate for species that become less selective the longer they search for suitable habitats, where habitat selection is relative to the quality and abundances of habitats in an area described by the searching radius of the organism. Alate aphids (winged migrants) behave in this way during their migratory and settling bouts (Kennedy 1975). MacArthur and Levins (1964) viewed habitat selection as a mechanism for species coexistence. Both *M. valerianl* and *A. varians* use fireweed during the summer months, but they differ in their preferences of feeding sites on the fireweed inflorescence (Addicott 1978).

Although my research concentrated on factors influencing between-plant habitat selection, rather than segregation of species on individual plants, species-specific differences found in the host selection may be ascribed to the effects of interspecific competition. If

competitor densities in good habitats are high enough to lower the expected fitness within good habitats, incoming *colonists should* avoid occupied habitats in favor of places that are of intrinsically lower quality, but that are of relatively greater quality because of the absence of competitors (Fretwell 1972).

B. Spatial scales -- what is a habitat?

In order to test hypotheses about the effects of habitat selection, it is first necessary to define what is meant by "habitat". The importance of defining habitat is even greater if the the role of habitat selection on two potentially competing species is to be studied. If two species discriminate among parts of the same environment on different spatial scales, the models of habitat selection discussed above may not be valid, or at least of less utility in describing the relationship between habitat selection and competition.

A definition of habitat put forward by Whittaker, Levin and Root (1973) requires that "habitat" be the part of an organism's physical and chemical environment to which the organism responds. Andrewartha and Birch (1954) mentioned three general uses of the term habitat, each defining a spatial scale within an organism's environment. Modified to match levels of organization within the aphid system these are:

1. the sort of country in which the animals are living,

e.g. fireweed plants.

2. the actual space occupied by a particular group of animals, e.g. a particular fireweed shoot.
3. the special sort of place which serves not for the whole life of the animal, but for one of its particular functions, e.g. breeding, feeding, sheltering (a particular part of the shoot, the inflorescence).

In this study of habitat selection, I will demonstrate that these aphid species respond to their fireweed environments in different ways. Scale 2 is appropriate for *A. varians*, while both scales 1 and 2 apply to *M. valeriani*, because of differences in the spatial scales over which these aphid species search for and select fireweed.

C. Literature Cited

Addicott, J.F. 1978. Niche relationships among species of aphids feeding on fireweed. Can. J. Zool. 56: 1837-1841.

Addicott, J.F. 1979. A multi-species aphid-ant association: density dependence and species specific effects. Can. J. Zool. 57: 558-569.

Andrewartha, H.G. and L.C. Birch. 1954. The Distribution and Abundance of Animals. Univ. Chicago Press, Chicago. 783 pp. Ch. 12.

Cody, M.L. 1981. Habitat selection in birds: the roles of vegetation structure, competitors, and productivity. Bioscience 31: 107-113.

Denno, R.F., M.J. Raupp, D.W. Tallamy, and C.J. Reichelderfer. 1980. Migration in heterogeneous environments: differences in habitat selection between the wing forms of the dimorphic planthopper *Prokelesia marginata* (Homoptera: Delphasidae). Ecology 61: 859-867.

Doyle, R.W. 1975. Settlement of planktonic larvae: a theory of habitat selection in varying environments. Am. Nat. 109: 113-126.

Elton, C. 1966. Animal Ecology. October House, New York. 227pp.

Fretwell, S.D. 1972. Populations in a Seasonal Environment. Princeton Univ. Press, Princeton, N.J. 217pp.

Fretwell, S.D. and H.L. Lucas. 1970. On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheor. 19: 16-36.

Hallett, J.G. 1982. Habitat selection and the community matrix of a desert small-mammal fauna. Ecology 63: 1400-1410.

Kennedy, J.S. 1975. Insect dispersal. In Pimentel, D.(ed). Insects, Science, and Society. Academic, New York. 284pp.

Krebs, C.J. 1978. Ecology: The Experimantal Analysis of Distribution and Abundance, 2nd ed. Harper and Row, New York

Lack, D. 1933. The psychological factor in bird distribution. Brit. Birds 31: 130-136.

Lack, D. 1937. Habitat selection in birds with special reference to the effect of afforestation on the Brechland avifauna. J. Anim. Ecol. 2: 239-262.

MacArthur, R.H. and R. Levins. 1964. Competition, habitat selection, and character displacement in a patchy environment. Proc. Nat. Acad. Sci. 51: 1207-10.

Rosenzweig, M.L. 1973. Habitat selection experiments with a pair of co-existing heteromyid rodents. Ecology 54: 111-118.

Rosenzweig, M.L. 1974. On the evolution of habitat selection. Proc. 1st Int. Congr. Ecol., pp. 401-404.

Rosensweig, M.L. 1981. A theory of habitat selection. Ecology 62: 327-335.

Whitham, T.G. 1978. Habitat selection by *Pemphigus* aphids in response to resource limitation and competition. Ecology 59: 1042-1052.

Whitham, T.G. 1980. The theory of habitat selection: examined and extended using *Pemphigus* aphids. Am. Nat. 115: 449-466.

Whittaker, R.H., S.A. Levin, and R.B. Root. 1973. Niche, habitat, and ecotope. Am. Nat. 107: 321-338.

II. Determinants of distributions in two co-occurring aphid species: habitat selection and spatial scales

A. Introduction

Animal distributions result from habitat selection by organisms and extrinsic factors that restrict individuals to a subset of suitable habitats. Some habitats with adequate resources for the maintenance of populations are nonetheless unoccupied because interspecific interactions, like competition and predation, limit population growth and survival in those habitats. There is a paucity of experimental work contrasting the roles of habitat selection and subsequent interactions in determining animal distributions. Despite this, many authors conclude that habitat selection is adaptive because animals are found in areas that provide the highest quality or greatest amount of resources (Cody 1981, Hallet 1982). Without experimental evidence, and without further experimentation to document how long habitats selected by organisms remain suitable after colonization, it is unclear whether or not animals select habitats optimally (Gould and Stinner 1984). This uncertainty has made it difficult to determine the relative contibutions of habitat selection and subsequent interactions in creating animal distributions.

Furthermore, few studies consider distances travelled by animals during the habitat selection process. Habitats vary in quality over a number of spatial scales (Southwood

1977, Gould and Stinner 1984). Unless animals search on a spatial scale large enough to encompass both good habitats with abundant resources and poor habitats where populations can exist only at low levels, the opportunity to select the habitats of the highest absolute quality would not arise. The scale of search by an animal might limit the number and kinds of places it is found. In some cases, animals are found in poor habitats within areas that have fewer resources than nearby areas, simply because their search distance is less than the distance between areas.

In the present experimental study of habitat selection and restriction, I examined four ecological attributes likely to affect the host selection and distributions of two aphid species that feed on the same host plant in similar ways: 1) intrinsic host plant quality, 2) inter- and intraspecific aphid densities, 3) ant attendance and 4) predation. I identified attributes chosen by the aphids, and compared them with those factors that affected distributions but did not elicit a response by the aphids. Experiments were designed to incorporate 3 spatial scales over which the aphids could make choices: among large areas, among plots within areas, and among plants within plots.

Biology of the aphid system

This study focused on alate (winged) *Aphis varians* Koch and both alate and apterous (non-winged) *Macrosiphum valeriani* (Clarke). During the summer, both species feed on

the inflorescence of fireweed (*Epilobium (=Chaemerion) angustifolium* L.: Onagraceae), a herbacious perennial. *Aphis varians* is ant-tended, disperses mainly by flying, and is less likely than *M. valeriani* to disperse by walking after settlement on a host plant (Antolin in prep.). *Macrosiphum valeriani* is not tended by ants, and disperses both by flying and walking (Addicott 1978a,1979, Antolin in prep.).

Aphids are capable of discriminating not only among different plant species (Kennedy et al. 1959, Annis et al. 1982), but also between different varieties of the same species (Muller 1958). The distribution of colonies on host plants, however, could simply be a statistical consequence of random settlement, high fecundity, and predation (Kennedy 1975, Shiyomi 1967, Bryant 1969). On the other hand, aphid performance decreases with increasing density, partially because of deterioration of plant quality at high aphid densities (Dixon 1977). Aphids arriving on plants with other aphids already present might respond to potential competitors and choose not to stay, perhaps moving to uncolonized plants of lower intrinsic quality (Whitham 1978).

Host plant quality, the first factor studied, dominates aphid host choice and distributions over a number of spatial scales (Kennedy and Fosbrooke 1972, Karieva 1983). The performance of aphid populations on individual host plants may be affected by variation in secondary compounds (van Emden 1972, Zucker 1982), levels of soluble nitrogen in

tissues and sap (van Emden and Bashford 1968, Mattson 1980), plant condition (turgor, chlorosis) and age (Kennedy 1958, Dixon 1977, Perrin 1976). Differences among areas in host plant density, dispersion and quality will affect movement of individuals and population dynamics at larger scales (Dixon 1977, Addicott 1978a, Karieva 1983).

In this experiment individual plant quality was not determined by any of the methods mentioned above. Addicott (Unpubl. data), however, has demonstrated that fecundity and development time in *A. varians* and *M. valeriani* are correlated with the total height of a fireweed shoot and the length of the inflorescence. In a study of the aphid *Uroleucon rudbecklae*, Service (1984) also found a correlation between aphid performamce and the height and vigor of its herbaceous host plant. Therefore, fireweed shoot height can be used as a predictor of plant quality.

The second factor examined, aphid density, could affect plant quality, and therefore, host choice. Because inter- and intraspecific aphid densities affect aphid performance negatively (see Dixon 1977 for a review, Addicott unpubl. data), plants with large aphid colonies might be avoided in favor of unoccupied plants. Aphid densities affect not only reproductive rates but also the degree of polymorphism (the proportion of winged migrants) within populations (Harrison 1980) and the probability of dispersal away from a plant (Walters and Dixon 1982). On the other hand, aphids may aggregate on host plants for at least three reasons. First,

many aphids feeding simultaneously create a nutrient sink, causing the plant to shunt resources to plant parts with aphids (Way and Cammell 1970). Second, aphids at high densities may better attract ants for tending (Way 1963, Addicott 1978c, 1979, Griffiths 1980). Third, aggregations of aphids may satiate predators before whole colonies are devoured (Kidd 1982).

The third and fourth factors, ants and predators, are related. Mutualistic relationships between ants and Homoptera have been documented extensively (e.g. Way 1963). Specifically, ant tending has positive effects on fecundity and survival of *A. varians* (Addicott 1978c, Griffiths 1980). Consequently, it is of interest to know whether *A. varians* search for plants where they gain protection from predators and increased reproduction as a result of ant tending. *Macrosiphum valeriani* should not respond to ants because ants do not directly interfere with this aphid (see Chapter III).

Natural enemies can cause dispersal from host plants (Addicott 1978a, Roitberg et al. 1979), and they significantly increase mortality, both within large areas and on single plants (Hagen and van den Bosch 1968, Sanders and Knight 1968, Perrin 1976). Major aphid predators on fireweed include coccinellid beetles, hymenopterous parasitoids, mites, anthocorid bugs, syrphid and chamaemyid fly larvae, and spiders. These predators could affect the distributions of both aphid species, by direct mortality or

by inducing aphids to disperse when attacked by predators.

The experiments reported here addressed four specific questions. First, do initially colonizing aphids discriminate between plants that differ in height (quality), or do aphids colonize indiscriminately? Second, what are the spatial scales of habitat choice, and do they differ between *M. valeriani* and *A. varians*? Third, how does habitat selection vary with aphid density? Finally, is host plant choice affected by the presence of ants and predators?.

In 1982, a colonization experiment was conducted to survey how host plant quality, aphid presence, and ants simultaneously affect aphid colonization. A removal treatment provided information about colonization as affected by plant quality and ants in the absence of resident aphids of either species. A second treatment, where colonizing aphids were left on plants after being marked, allowed analysis of the effects of intra- and interspecific aphid densities on colonization by comparing settlement in removal plots with settlement in marking plots. Furthermore, by using a number of areas, this experiment examined several spatial scales over which host choices could be made. The response and impact of predators was examined in 1983.

B. Study sites and methods

Study areas were located along Coal Creek, 2-4 km west of Crested Butte (107°01' West, 38°52' North, elev. 2804m), in the Gunnison National Forest, Gunnison County, Colorado,

U.S.A.

1982 experiment

Five areas with abundant fireweed were divided into 1.0 m^2 plots. Plots were chosen by laying a transect through areas of fireweed, and by designating plots adjacent to either side of the transect. There were 55 one meter-squared plots that included fireweed, and all of these were used. In this way, 50-90% of the fireweed shoots in the study areas were included in the experiment. Plot densities ranged from 4-41 fireweed shoots per m^2.

The plots were divided into two treatment groups: removal and marking (Figure 1). Plots were ranked according to density and were alternately assigned to treatments by fireweed density ranks. This led to interspersion of treatment plots, so that the problems of improper treatment interspersion, as pointed out by Hurlbert (1984), were avoided. Each treatment had plots with a similar range of shoot densities. A total of 981 fireweed shoots were monitored, 489 in 28 removal plots, and 492 in 27 marking plots. One plot in the marking treatment and one shoot in the removal treatment were lost during the colonization experiment because of trampling (by intruding cattle). There were 970 shoots included in the analyses of fireweed height; 482 in marking plots, and 488 in removal plots.

In removal plots all colonizing aphids were removed, while in marking plots colonizing aphids were dusted with a

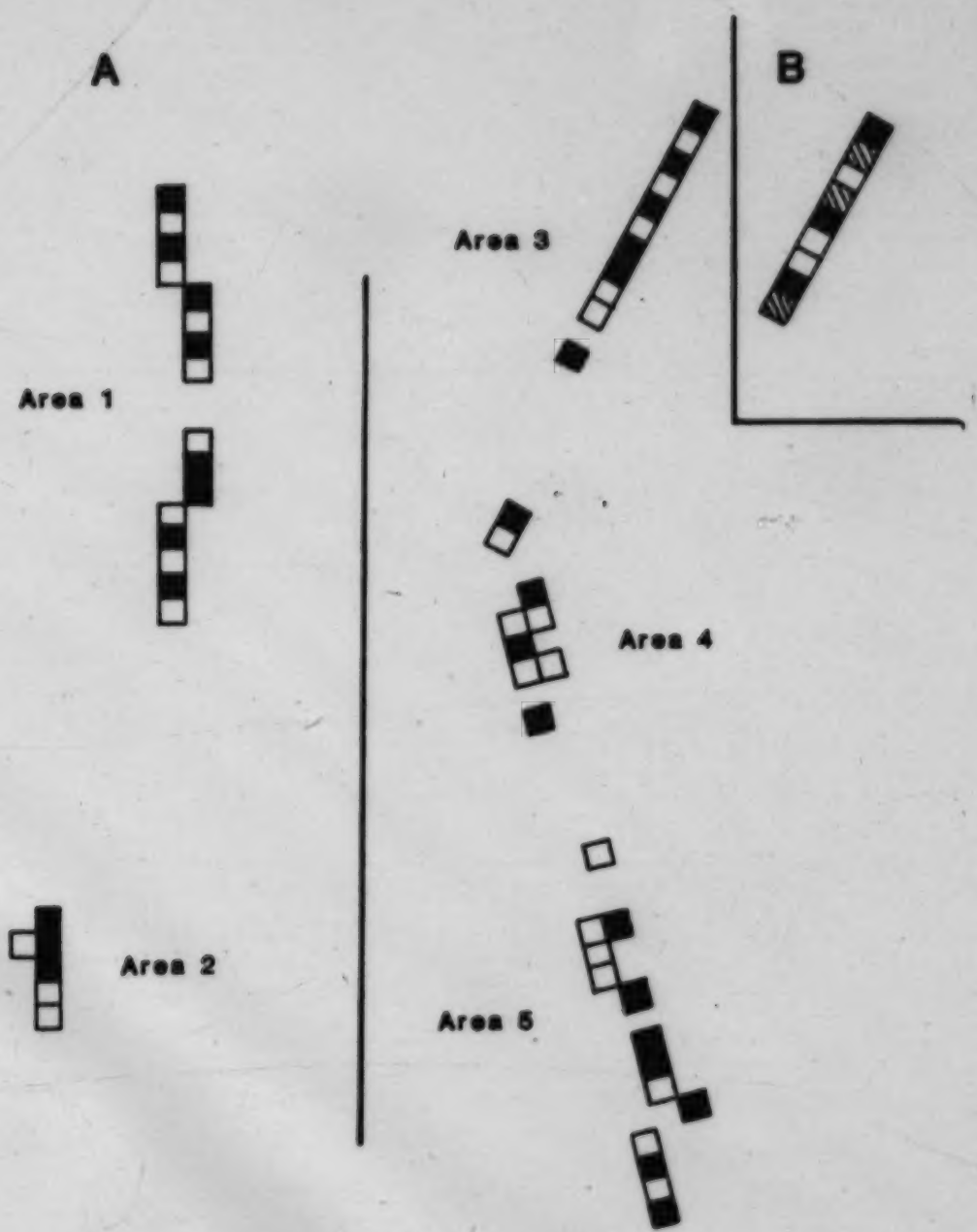


Figure 1. Areas and plots of experiments. Each plot is 1m². A.) 1982; dark plots removal, white plots marking; treatments were interspersed. The figure reflects the actual distances between areas 1 and 2, and among areas 3, 4 and 5. Areas 1 and 2 were 2km west of areas 3 to 5. B.) Area 3 where 1983 experiment was carried out. Dark plots *A. varians* addition, white plots *M. valerianl* addition, hatched plots control.

flourescent powder but were left on the fireweed. The color powder marks on the aphids faded quickly, because of almost daily afternoon rainshowers, but marks could still be found along the wingveins on the aphids by looking closely with a 10x hand lens.

Aphids were first seen on fireweed on July 1, 1982 and experiments began on July 8. Plots were sampled at four day intervals. An initial survey before the beginning of the experiment indicated that a shorter time period would have yielded too few data per sample. A longer sampling period would have made the loss of information likely because some colonizing aphids may have been killed by predators between samples. Those predation events would have gone undetected. A 4 day sampling period decreased the chance of missing aphid colonizations.

The sampling period continued for 18 days, so that five samples were taken. This period included the majority of the initial movement of aphids from their respective winter hosts to fireweed. The experiment was halted when colonizations drastically decreased after the fifth sampling period (see Figure 2). Removal plots were sampled from July 8 to July 24, marking plots were sampled from July 10 to July 26.

When an aphid was found on a fireweed shoot, it was necessary to have criteria for determining whether or not a final choice had been made because aphids may sample several plants during host searching. Aphids were considered to have

colonized if their stylets were inserted into the plant tissue, or if offspring were present.

In addition to the numbers of aphids counted on each shoot, the presence of ants and five kinds of predators was noted. Predators were not further considered for 1982, because their presence was recorded only on fireweed shoots that had been colonized by the aphids, rather than on all shoots.

At the end of the experiment, the height of each fireweed shoot was measured. It is assumed that measurements at the end of the period accurately reflected relative fireweed shoot heights during the experiment. In addition, the height of other vegetation in each plot was measured at nine uniformly spaced points. The mean of the nine measurements yielded a measure of height of surrounding vegetation in the plot and an index of fireweed exposure, defined as an individual shoot's height minus average vegetation height in the surrounding plot.

1983 experiment

A subset of the same plots was used for an aphid addition experiment, designed to further test the effects of interspecific and intraspecific aphid densities on colonization (Figure 1B). The purpose of this experiment was to test colonization on fireweed shoots with aphid densities greater than those observed during the initial colonization phase in the 1982 experiment. Because there was little

natural colonization by alates of either *M. valerianl* or *A. varians* at this site during the summer of 1983, colonization data were not sufficient for analysis in this experiment. This experiment, however, provided an opportunity for measuring the responses and impact of predators.

All fireweed was cut down outside the study plots, to maximize colonizations in experimental plots by forcing all colonists onto the plots. The following three treatments were used: addition of *A. varians* to all fireweed shoots within a plot, addition of *M. valerianl* to all shoots, and aphid removal. The plot treatments were interspersed randomly in a block design; each block was a group of 3 consecutive plots along the transect. Fireweed shoots within plots were culled so that the three treatment plots within a block had the same plant density. Three blocks, containing a total of 120 fireweed shoots, were used in the experiment.

There were two additions of aphids and four censuses. On July 28 and 29, apterous aphids were collected from fireweed at other sites, and directly transferred onto fireweed in the experimental plots in net bags that were tied over the fireweed inflorescences. There were 5-10 aphids placed in each bag. The net bags were removed the following day, and the plots were sampled for alate colonists and apterous survivors on August 1 and again on August 3. On August 5, aphids were again bagged onto fireweed shoots with an inflorescence, and bags were removed the following day. The plots were censused on August 8 and

again on August 12. At each census, the numbers of added aphids, any colonists, and any predators present on the fireweed were recorded.

C. Results

1982 experiment

In this experiment, three spatial scales were differentiated: large areas of fireweed, plots within areas and individual fireweed shoots within plots. In order to make meaningful conclusions about the effects of spatial heterogeneity on host selection by the aphids, environmental variation at each of the spatial scales was characterized. The response by aphids to fireweed was examined at all of these spatial scales. Interspecific and intraspecific aphid effects were analyzed on the scale of individual fireweed shoots only, while the effects of ants were considered on the scale of plots only. In turn, selection by the aphids was equated to the levels of host plant variation, and finally, how the presence of aphids and ants altered host selection was examined.

Spatial scales and host plant effects

The five study areas differed in average fireweed shoot height (Table 1); Area 3 had much larger plants than the other areas (Student-Newman-Keuls, $P < .05$). Average fireweed shoot height was similar in areas 2, 4 and 5; Area

Table 1 -- A.) Two-way nested analysis of variance of fireweed shoot height at two spatial scales (areas, plots) and between treatments. ** p<.001. B.) Mean plant heights in the areas, compared by Student-Newman-Keuls. Means with the same number subscript do not differ. Values (cm) were log transformed to stabilize the variance.

A.)

Source	d.f.	MS	F
TREATMENTS	1	0.01	0.11
AREAS	4	1.43	10.84 **
TREATMENTxAREA	4	0.05	0.41
PLOTS	44	0.13	7.27 **
RESIDUAL	916	0.02	
TOTAL	969		

B.)

Area 1	Area 2	Area 5	Area 4	Area 3
46.03_1	$62.23_{1,2}$	$65.61_{2,3}$	66.22_3	88.31_4

1 had the smallest fireweed. Overall, there was significant variation among plots within treatments and areas, but there were no differences in shoot size between treatments. The interaction between areas and treatments also was not significant (Table 1), indicating that marking and removal plots had shoots of equal height within each area.

Temporal patterns of colonization over the course of the experiment differed between the two species (Figure 2). Throughout the experiment, *A. varians* colonization was fairly low, but constant. Colonization by *M. valeriani* was at first similar to *A. varians*, but increased dramatically during the third, fourth and fifth sampling periods. The experiment included the majority of colonization of fireweed at the beginning of the season, when the aphids were first moving from their winter hosts (*Rosa* spp. for *M. valeriani* and *Ribes* spp. for *A. varians*).

Areas

The numbers of aphids colonizing per plant did not significantly differ among areas for *A. varians*, but did differ for both alate and apterous *M. valeriani* (Table 2). Many *M. valeriani* alates were found in Area 3, the area with the tallest (highest quality) fireweed shoots. Area 4, which was colonized by many *M. valeriani* apterae, was adjacent to a group of rose bushes (the winter host) that had large *M. valeriani* colonies on them. It is likely that many apterous colonists walked from the rose bushes into that nearby area.

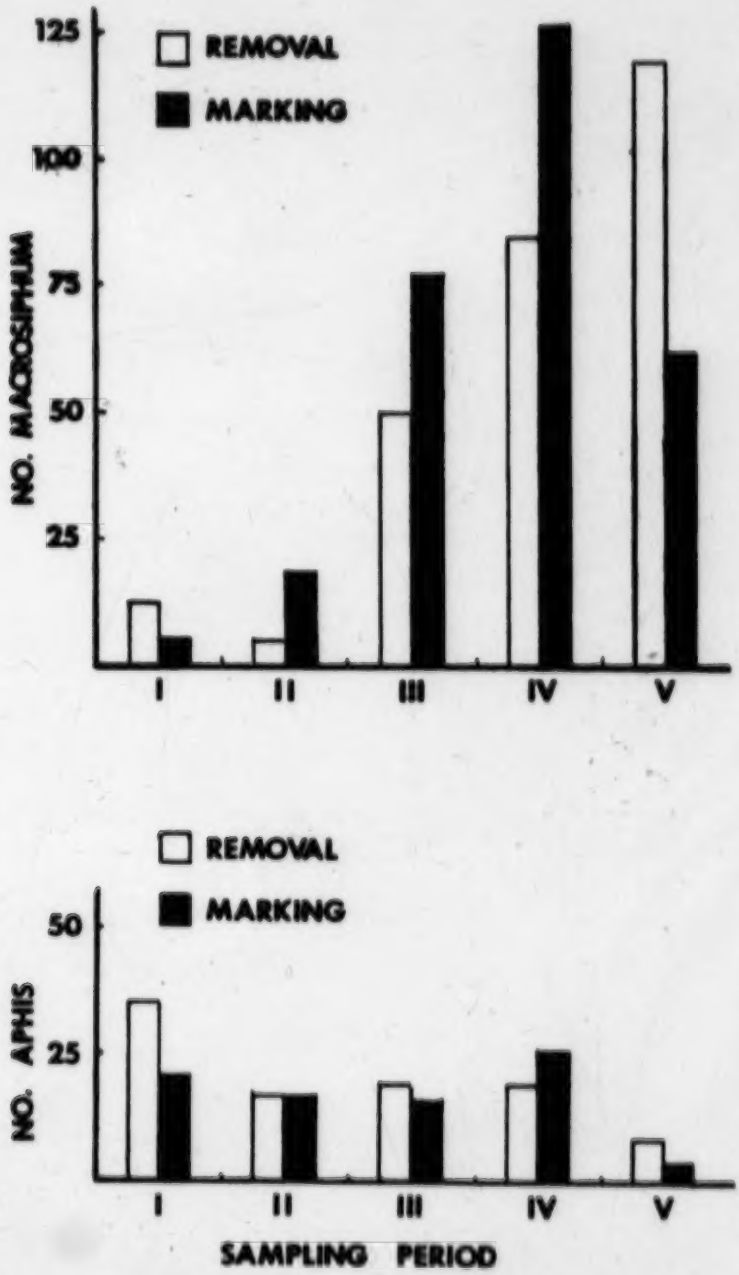


Figure 2. Distributions of colonizations by *M. valeriani* and *A. varians* at each sampling period during the 1982 experiments.

Table 2 -- The numbers of fireweed shoots (plots), shoots colonized, and numbers of aphids colonizing per sheet in the five areas. Kruskal-Wallis ANOVA tests for differences in numbers of colonists per shoot among areas. † 4 d.f., P<.05

M. valeriani

		alates		apterae	
	Total shoots (#plots)	Number of shoots colonized	Number colonizing per shoot	Number of shoots colonized	Number colonizing per shoot
Area 1	247 (16)	40	.36	9	.13
Area 2	79 (6)	12	.19	1	.01
Area 3	128 (10)	47	.92	6	.06
Area 4	151 (9)	28	.42	37	.60
Area 5	366 (14)	89	.35	4	.01

Kruskal-Wallis H: alates, H = 14.24 †; apterae, H = 18.06 †

A. varians

	Total shoots (#plots)	Number of shoots colonized	Number colonizing per shoot
Area 1	247 (16)	35	.20
Area 2	79 (6)	18	.28
Area 3	128 (10)	29	.24
Area 4	151 (9)	22	.21
Area 5	366 (14)	31	.12

Kruskal-Wallis, H = 7.61

Aphis varians colonization was correlated with the number of fireweed shoots within each area (ρ=.90, P=.05), indicating that *A. varians* does not distinguish habitat quality among areas, but colonizes in a "rain" proportionately to the size and density of a particular area of fireweed. No correlations between the numbers of *M. valeriani* and fireweed height or density were significant, even though more *M. valeriani* alates were found in the Area 3. If *M. valeriani* alates colonize the largest fireweed within ≈10 m of their winter hosts, the high numbers of *M. valeriani* colonizing Area 3 could be due to its proximity to area 4 and the rose bushes with large *M. valeriani* colonies (see Figure 1),

Plots

Aphid colonization has been described as a random process (Shiyomi 1967, Bryant 1969). To test whether colonization by *M. valeriani* and *A. varians* is nonrandom on the scales of plots and individual fireweed shoots, a null model of colonization was constructed. The model was used to test whether settlement by both forms of *M. valeriani* and alate *A. varians* differed from random. Using the distribution of colonization over the five sampling periods, as observed during the experiment (see Figure 2), and assuming that each plot and each fireweed shoot in all the areas had an equal chance of being colonized, expected distributions of aphids colonizing both plots and individual

fireweed shoots were generated. Expected numbers of colonists in each plot during each sampling period and the expected numbers of colonists in each plot over the course of the whole experiment were calculated. This was done by randomly assigning aphids to individual fireweed shoots using a computer simulation of colonization. The "experiment" was repeated 1000 times, and expectations were found by taking the mean of all 1000 iterations. The simulation derived both the numbers of aphid colonists in each plot over the course of the whole experiment, and expected numbers of colonists on each plant during each sampling period. The model included the possibility that many aphids colonize the same shoot during a single sampling period.

Aphis varians colonization into plots did not differ from the null model, but settlement by *M. valeriani* alates and apterae into both the marking and removal treatment plots differed from random expectation (Figure 3). *Macrosiphum valeriani* colonized a small number of plots more often than expected by random, and did not colonize many more plots than expected.

To identify habitat variables that were associated with non-random settlement in the plots, correlation coefficients between the numbers of aphids colonizing plots and plant density, average height, and average exposure per plot were calculated (Table 3). The only significant result showed that more *M. valeriani* alates settled in plots with exposed

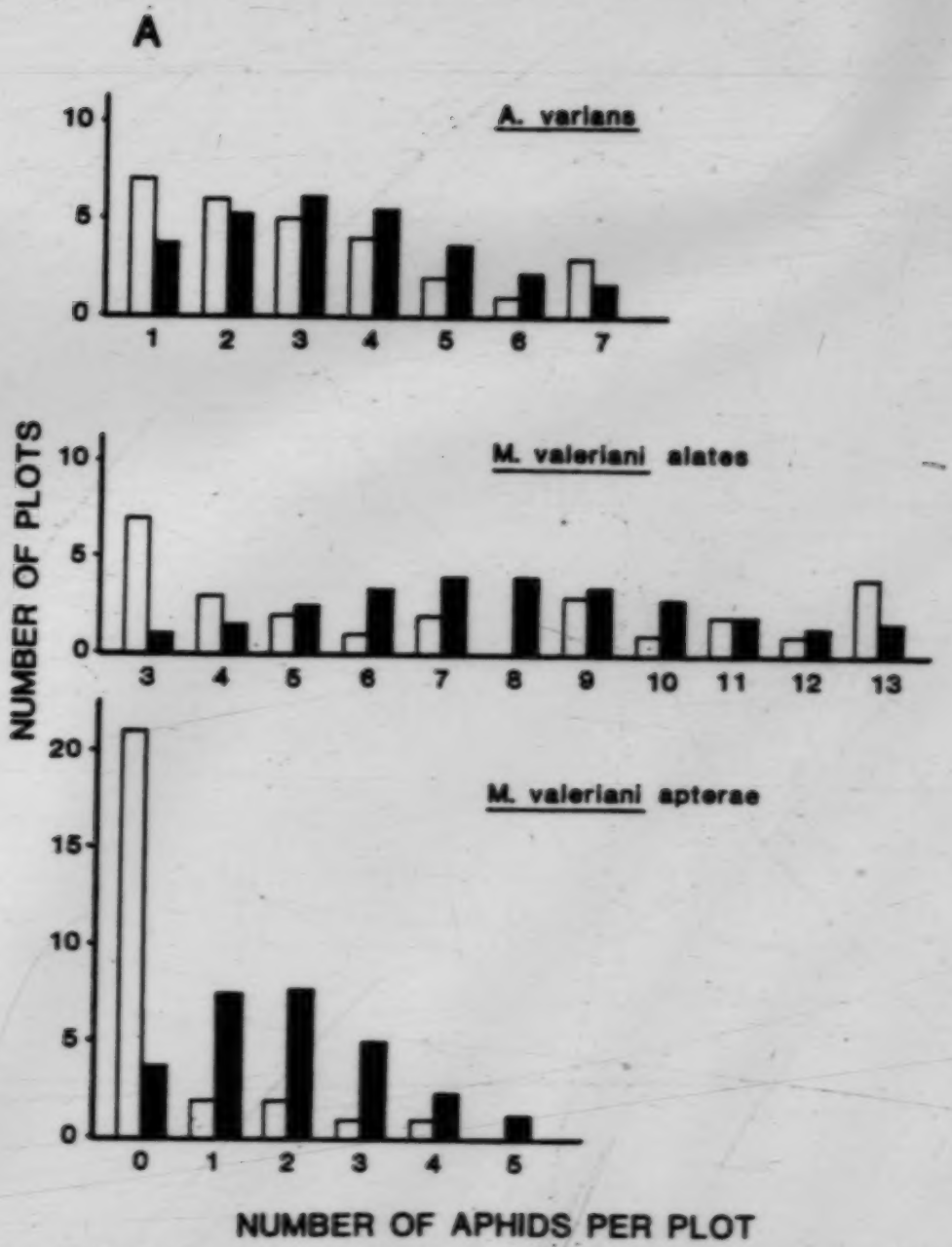


Figure 3. Comparison between observed distributions of aphids colonizing plots (open bars) over the course of the whole experiment and distributions expected (dark bars) under a random colonization model (see text for description). Some categories on the left and right sides of the distributions have been grouped. A.) Removal plots: *A. varians*, χ^2=6.37, 6 d.f., P>.10; *M. valeriani* alates, χ^2=45.41, 10 d.f., P<.001; *M. valeriani* apterae, χ^2=92.93, 5 d.f., P<.001.

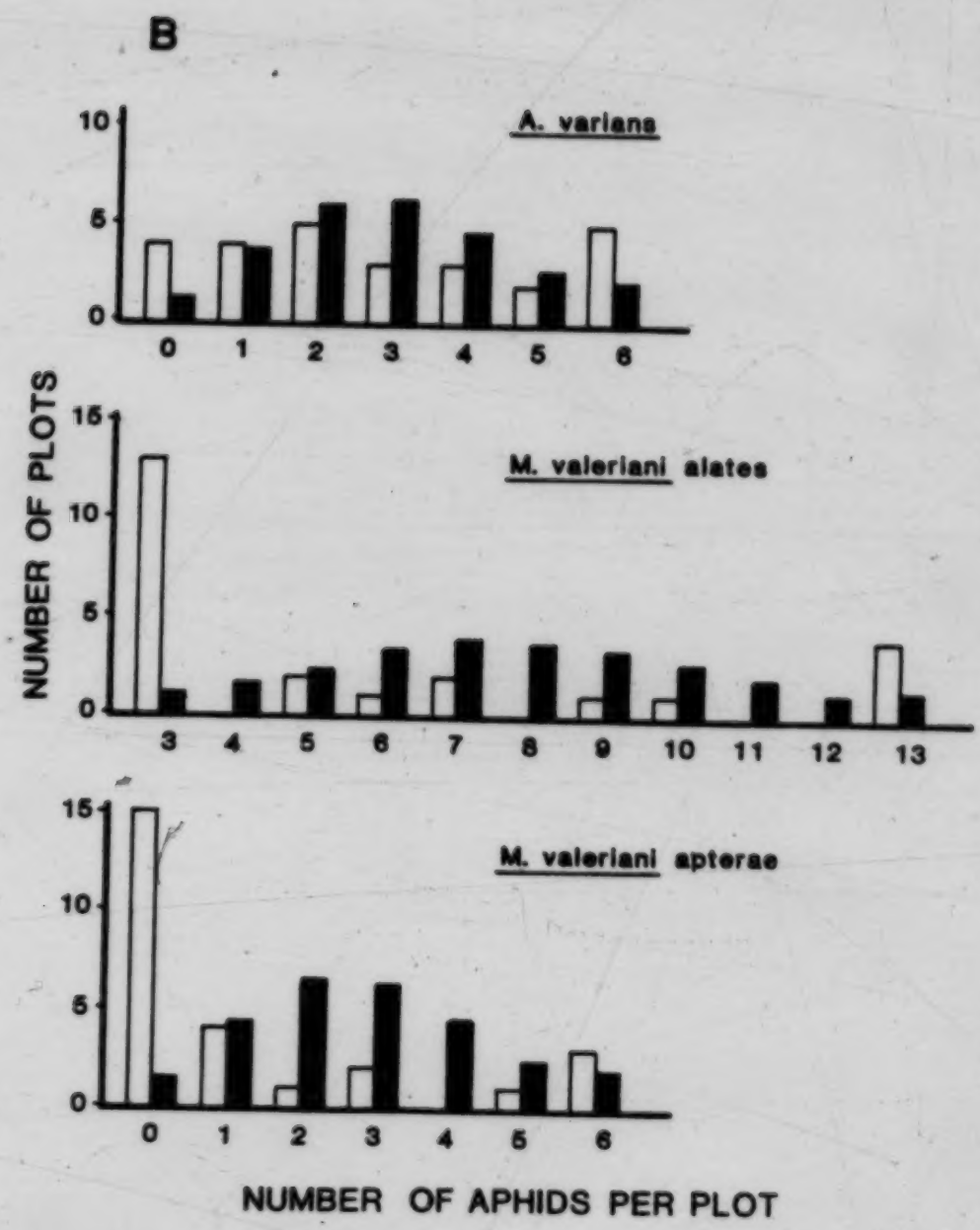


Figure 3B.) Marking plots: *A. varians*, χ^2=11.81, 6 d.f., P>.05; *M. valeriani* alates, χ^2=146.50, 10 d.f., P<.001; *M. valeriani* apterae, χ^2=138.17, 6 d.f., P<.001.

Table 3 -- Rank correlation coefficients between plot characteristics and the numbers of aphids that colonized each plot. 28 removal plots, 26 marking plots. * p<.05

	Number of shoots	Average height	Average exposure
M. valerianl alates			
Removal	.269	0.296	0.499 *
Marking	0.056	0.095	0.515 *
M. valerianl apterae			
Removal	0.108	0.083	-.046
Marking	-.021	-.167	0.309
A. varians			
Removal	0.017	0.248	0.265
Marking	-.121	-.072	0.223

fireweed from both marking and removal treatments. Alate *M. valeriani* colonization was not correlated with either fireweed shoot height or fireweed density. Nonrandom colonization cannot be explained for *M. valeriani* apterae, other than that apterae moved onto plants near their winter hosts. *Aphis varians* colonization was not affected by variation in fireweed density, exposure or height among plots.

Individual fireweed shoots

To test whether colonization of individual fireweed shoots was nonrandom, two analyses of the removal experiment data were carried out. Expected patterns of recolonization of fireweed shoots and the numbers of aphids arriving on each shoot during each sampling period were generated using the same random colonization model described above. Random expectations were compared to observed colonization.

The first analysis indicated that *A. varians* and both alate and apterous *M. valeriani* colonized fewer fireweed shoots than expected from the random model (Figure 4). Those shoots that were never colonized and the fireweed shoots that were recolonized several times during the removal experiment were more frequent than expected. In the second analysis, multiple colonizations (where two or more aphids arrived simultaneously on the same fireweed shoot) were much more common than expected (Figure 5). *Macrosiphum valeriani* and *A. varians* prefer a subset of the fireweed; colonization

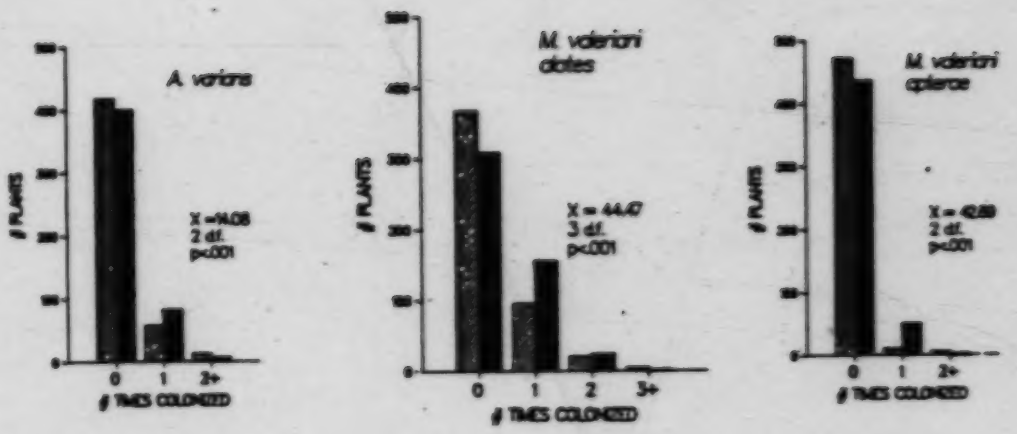


Figure 4. Comparison between observed distributions of numbers of colonizations of fireweed shoots (cross-hatched bars) and the expected distribution (dark bars) generated from a model of random colonization (see text for description of model). Data from removal plots used in this analysis.

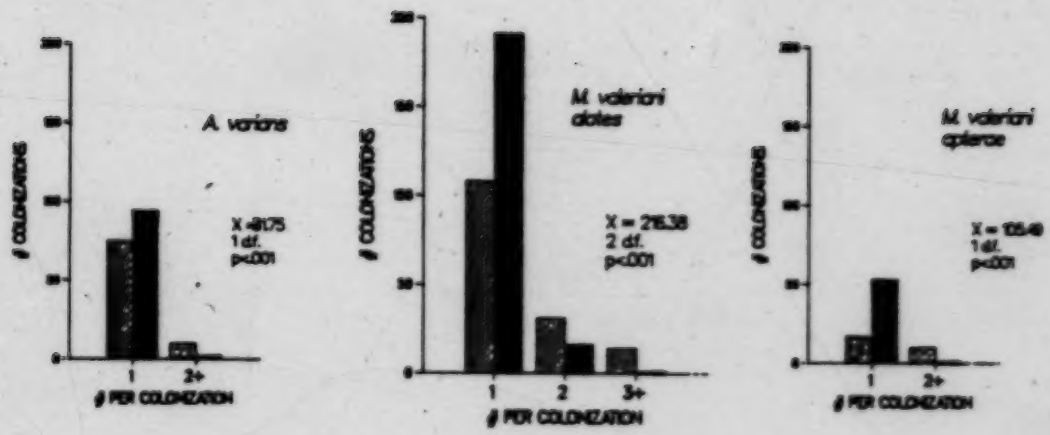


Figure 5. Comparison of observed distributions (cross-hatched bars) of types of colonizations (one aphid colonizing in each sampling period, two aphids, etc.) on fireweed shoots with the distribution expected (dark bars) if colonization were random (see text for description of model).

of individual fireweed shoots by both species is nonrandom.

A comparison of heights of colonized and uncolonized fireweed showed that both species differentially colonized large fireweed (Figure 6). Both alate and apterous *M. valeriani* were found on large fireweed (alates t=11.73, apterae t=3.17; 968 d.f., P<.001). Because both forms of *M. valeriani* settled on tall individual fireweed shoots, alate and apterous *M. valeriani* will be considered together in all subsequent analyses. The same result was found when fireweed exposure was compared between colonized and uncolonized plants. Exposure is defined as the height of a fireweed shoot, minus the average height of surrounding vegetation.

To test whether *M. valeriani* and *A. varians* colonists were associated with both fireweed height and exposure, a number of three way contingency tables were constructed. The analysis of multi-way frequency tables, similar to analysis of variance and based on a log-linear model, detects higher order interactions among factors without the rigid assumptions of regression and analysis of variance (Feinberg 1970, Addicott 1979). Models of expected frequencies that include the direct effects of each variable and all possible higher order interactions among variables are generated. Each model is compared to observed frequencies by the log likelihood ratio statistic (G^2). The analysis provides both a best-fit model and a test of significance for each term within each model. Three-way tables were constructed for each species using plant height (HGT), plant exposure (EXP),

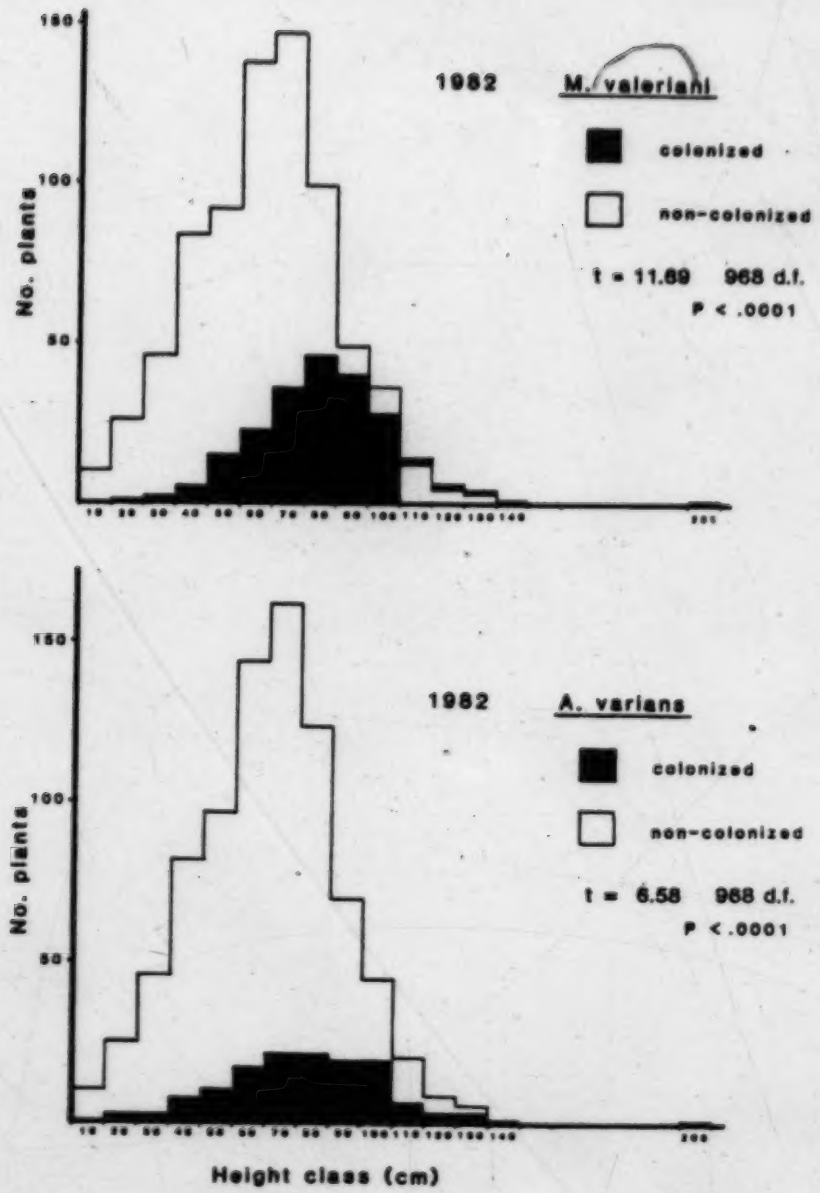


Figure 6. Distribution of colonized and uncolonized fireweed shoots in 1982. Means are: *M. valeriani* colonized 81.58cm, uncolonized 62.30cm; *A. varians* colonized 78.96cm, uncolonized 64.96cm.

and whether a plant was colonized or not (COL). Height and plant exposure were categorized into quartiles. If aphid colonization was affected simultaneously by height and exposure, the log-linear model with a three-way (HGT x EXP x COL) interaction should be significant.

For both species, the model that included all two way terms was a good fit, but for *M. valeriani* the three-way interaction was also significant (G^2=18.99, 9 d.f.,P<.05). The three-way term for *A. varians* was close to significance (G^2=15.12, 9 d.f., P>.08). *Macrosiphum valeriani* colonized large shoots more frequently than small plants, except when surrounding vegetation was tall as well (Figure 7). Small plants in low or sparse vegetation (i.e. with greater exposures), were more frequently colonized than those small plants that were not exposed. The same trend appeared for *A. varians*, but the relationship was not as strong.

Effects of aphids

I explored the response of colonizing aphids to the presence and densities of resident aphids in two ways. First, colonization in the marking treatment was compared to colonization in the removal treatment, using two-way and multi-way contingency table analyses. If the aphids avoided one another, colonization should have been more frequent on plants in the removal experiment, where more unoccupied fireweed shoots were available. If they aggregated, fireweed should have been colonized more frequently in marking plots

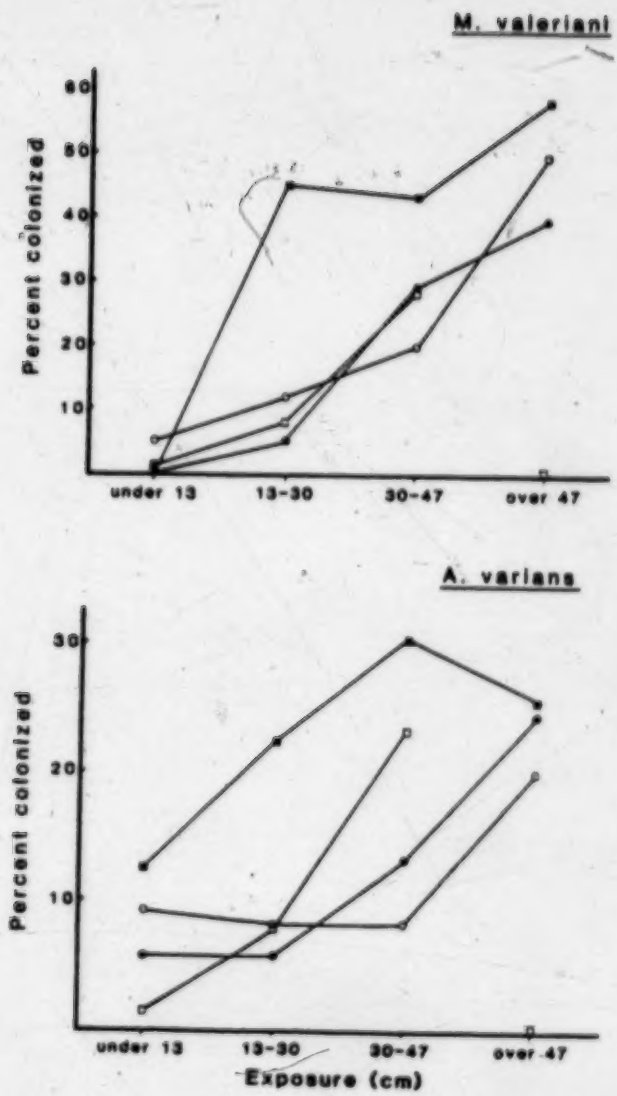


Figure 7. Interaction between fireweed shoot height and height relative to surrounding vegetation (exposure). shoots under 52 cm, • between 52 and 66.9 cm, o 67 and 81.9 cm, ▪ shoots 82 cm and over. Only two plants in the smallest height category fell into the largest exposure category.

than in removal plots.

The second analysis examined the relationship between colonization and resident population size, using data from the marking treatment only. Within the marking treatment, the numbers of aphids colonizing should be either positively correlated with densities of aphids present if the aphids aggregate, or negatively correlated if aphids avoid each other. Alternatively, there might be no relationship between resident density and numbers of new colonists.

The first analysis comparing treatments tested for differences between distributions of recolonizations in each of the treatments (in how many of the five samples each plant was recolonized). There was neither a positive nor a negative differential response between removal and marking treatments (Figure 8: *M. valeriani*, χ^2=6.60,3 d.f.,P>.10; *A. varians*, χ^2=0.68,2 d.f.,P>.90). No fireweed were colonized in all 5 sampling periods, and only 4 shoots were colonized 4 times, always by *M. valeriani*.

The second comparison between treatments examined the total number of aphids that colonized each individual fireweed shoot over the course of the whole experiment. A three-way contingency table analysis was carried out to determine whether the total number of aphids colonizing fireweed in the two treatments was affected by fireweed shoot height. Three-way tables, using fireweed shoot height (HGT), treatment (TREAT), and number of aphids colonizing (NCOL) were examined. There were no differences between

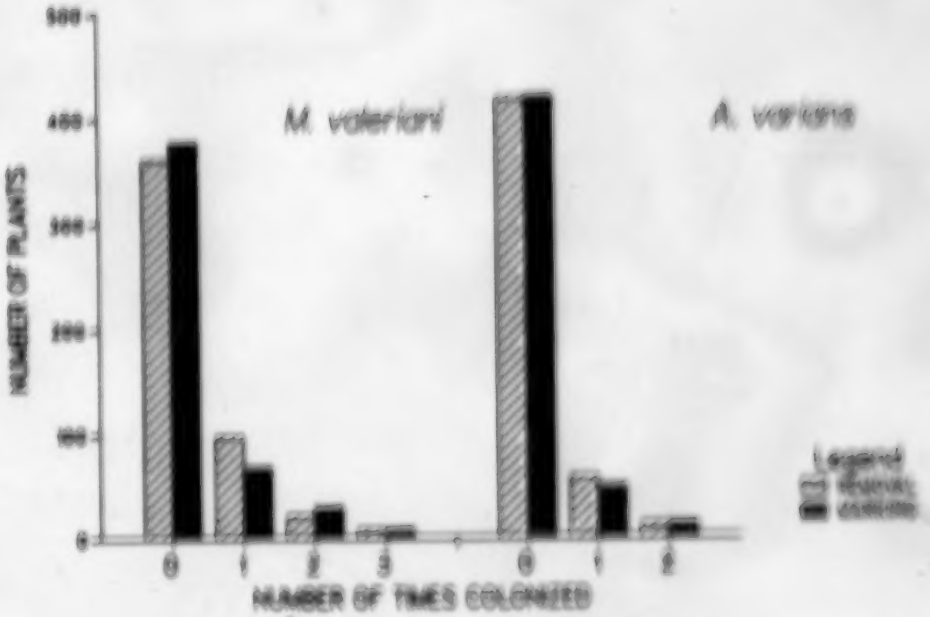


Figure 8. Comparison of number of sampling periods in which fireweed shoots were colonized between marking and removal treatments.

treatments; none of the best-fit models for either aphid species included a TREAT direct effect or interaction term. NCOL x TREAT terms were not significant, and therfore did not improve the fit of the models (*M. valerianl*, $G^2 = 4.24$, $P>.10$, *A. varians*, $G^2 = 1.35$, $P>.50$). Not surprisingly, best-fit models for both species included a HGT x NCOL interaction, since aphids prefer taller fireweed plants.

Another contingency table analysis was used to demonstrate more clearly that there were no interspecific or intraspecific aphid effects. This test examined the null hypothesis that the preference or avoidance of a fireweed shoot was not influenced by the presence of aphids. The number of aphids arriving over 4-day sampling periods (one, two, three or more etc.) were compared between the marking and removal treatments. Data from the marking treatment were divided into four categories: unoccupied plants, plants with just *M. valerianl* or *A. varians* present, and fireweed with both species present (Table 4). First, notice that few colonizations occured on fireweed shoots with other aphids on them, and second, that the frequency of types of colonizations did not change under the condition that aphids were already present on the plant.

Finally, correlation coefficients between the numbers of aphids colonizing, and the numbers of aphids present were calculated for fireweed shoots within the marking treatment (Table 5). Only the last three sampling periods were examined, since aphid populations did not build up until

Table 4 -- Types of colonizations (single, double, or greater) on fireweed shoots from removal plots (unoccupied shoots) and from four categories of shoots in the marking plots. † This category was not included in the analysis because expected frequencies were less than 1.

Colonization by *Macrosiphum valeriani*

Number colonizing	Removal	Marking plots			
		Neither present	*M.v.* present	*A.v.* present	Both present
1	110	60	16	11	3
2	37	20	7	2	2
≥3	21	13	6	5	3

$\chi^2 = 8.33$, 8 d.f., $P>.30$

Colonization by *A. varians*

Number colonizing	Removal	Marking plots			
		Neither present	*M.v.* present	*A.v.* present	Both present
1	75	46	8	10	1 †
≥2	10	3	1	3	0

$\chi^2 = 2.86$, 3 d.f., $P>.30$

Table 5 -- Interspecific and intraspecific (Spearman rank) correlations between numbers of aphid colonists and resident density. † Correlation is not defined.

Colonist	Resident	Time period	ρ (N)	Sig.
M.valeriani	*A.varians*	July 14-18	.231 (38)	n.s.
M.valeriani	*A.varians*	July 18-22	-.096 (53)	n.s.
M.valeriani	*A.varians*	July 22-26	.341 (37)	P<.05
A.varians	*M.valeriani*	July 14-18	-.269 (14)	n.s.
A.varians	*M.valeriani*	July 18-22	-.021 (23)	n.s.
A.varians	*M.valeriani*	July 22-26	---- (2)	†
M.valeriani	*M.valeriani*	July 14-18	.422 (38)	P<.05
M.valeriani	*M.valeriani*	July 18-22	.096 (53)	n.s.
M.valeriani	*M.valeriani*	July 22-26	.061 (37)	n.s.
A.varians	*A.varians*	July 14-18	.139 (14)	n.s.
A.varians	*A.varians*	July 18-22	-.179 (23)	n.s.
A.varians	*A.varians*	July 22-26	---- (2)	†

late in the experiment. Of the twelve (interspecific and intraspecific) comparisons made, only two were significant, eight showed no relationship, and two others had too few colonizations to allow analysis. Of the eight non-significant correlations, equal numbers had positive and negative signs. As there was no consistent pattern, correlation in this case provided no evidence for response to potential interspecific or intraspecific competitors by either aphid species.

Effects of ants

The effects of ants were analyzed on the plot level. Plots were divided into two categories, those that had ants foraging in them during one or more sampling periods, and those in which ants were never observed. The assumption was made that if ants were found on one shoot in a plot during a census, all shoots in that plot had ants foraging on them at some time. Four ant species foraged on fireweed plants at Coal Creek: *Formica fusca* Linnaeus, *F. cinerea lepida* Wheeler, *Tapinoma sessile* (Say), and one species from the *Formica rufa* group, either *F. integroides* or *F. obscuripes*. *Aphis varians*, which is ant tended, was expected to preferentially colonize plots with ants foraging in them, while *M. valeriani* was expected to avoid plots with ants. 11 of 28 removal plots and 10 of 27 marking plots had ants foraging in them (Figure 9). Ants did not noticably affect numbers of colonizations by either aphid species in plots

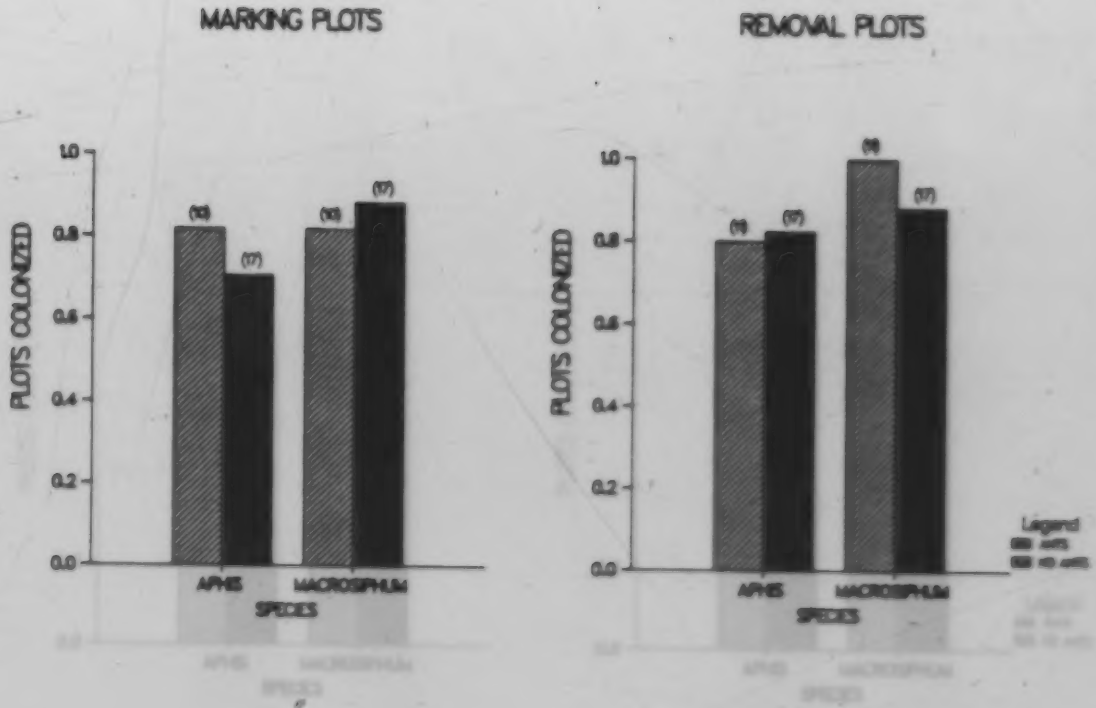


Figure 9. Proportion of plots with ants present or absent that were colonized by either aphid species. Numbers in parentheses above the bars indicate how many plots did or did not have ants.

from either treatment (Marking: *M. valeriani*, χ^2=.863,1 d.f.,P>.35, *A. varians*, χ^2=.624,1 d.f.,P>.40; Removal: *M. valeriani*, χ^2=1.27,1 d.f.,P>.25, *A. varians*, χ^2=.231,1 d.f.,P>.80). There was no pattern found -- neither preference for ant tended areas by *A. varians*, nor avoidance by *M. valeriani*.

1983 experiment -- effects of predators

The most common predators at Coal Creek were mites, anthocorid bugs and spiders, although hymenopterous parasitoids and syrphid flies were seen as well. The data from this experiment demonstrated that predators responded quickly to increasing aphid densities and caused significant mortality. The response of aphids to predators could not be directly examined using these data, as there was no natural colonization during the experiment.

Predator response to fireweed shoots with *A. varians* was quite marked, compared to the response on control shoots and on shoots with *M. valeriani* (Figure 10). High visitation rates by predators resulted in high mortality for *A. varians* -- many dead aphids were found on the plants. In *A. varians* addition plots, only 9 of 40 shoots still had live *A. varians* five days after the aphids were initially bagged onto the plants. Only 12 of 40 artificial colonies were still intact 7 days after the second addition. Few *M. valeriani* were found on either fireweed shoots in the experimental plots or on shoots in adjacent plots. Only 3 of

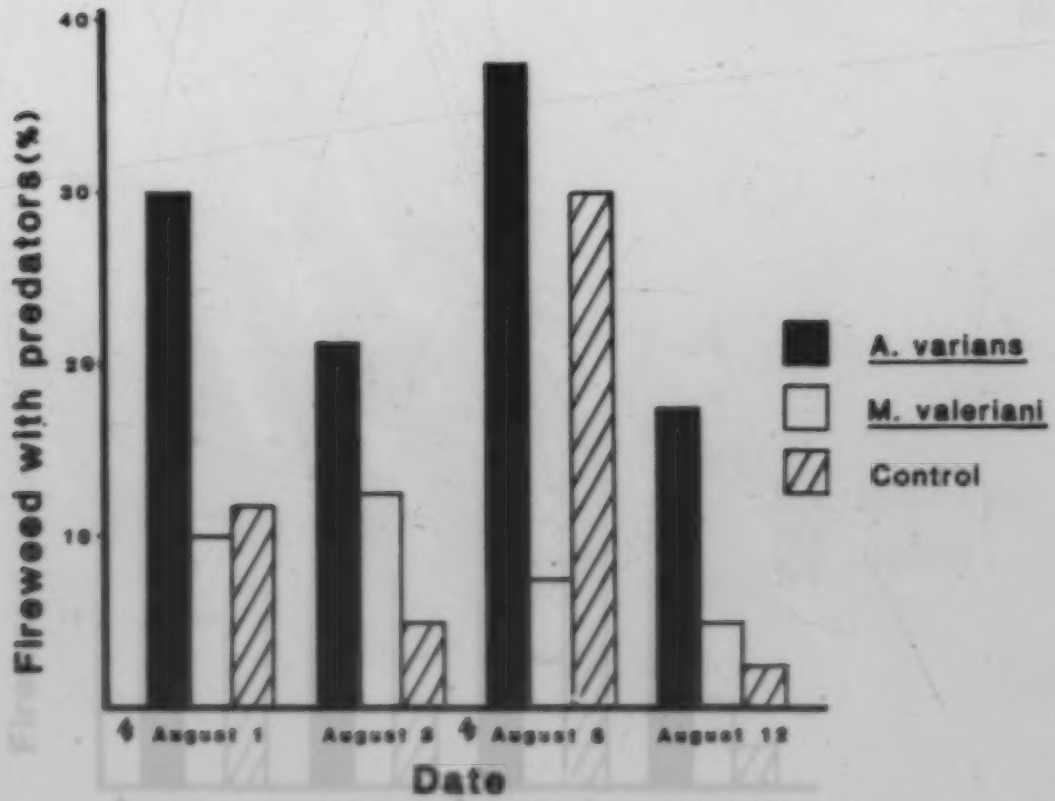


Figure 10. Predator's response to aphids in the 1983 experiment. Arrows indicate when aphids were artificially colonized onto the plants.

40 *M. valeriani* colonies were found after the first addition, and again only 3 of 40 colonies remained after the second addition.

These data were analyzed by a three-way contingency table, using treatment (TREAT), predator presence/absence (PRED), and time (TIME). Samples were considered independent because predators were removed at each census. The model with the fewest terms that provided a significant fit to the data contained only a PRED x TREAT interaction term (G^2= 22.63, 18 d.f., P > .20) , although the model including both the PRED x TIME and the PRED x TREAT terms was also a good fit. PRED x TIME terms (G^2 = 13.41, 6 d.f., P<.05) and PRED x TREAT terms (G^2 = 20.99, 4 d.f., P<.001) were both significant. The significance of these terms supports the observation that the densities of predators differed between treatments, and that as the aphids were depleted after introduction, predators became less common on all plants.

Furthermore, before the aphid addition predators were evenly distributed among the three treatments. In a census taken on July 27, before aphids were introduced, there were no differences among treatments in the numbers of fireweed with predators (x^2=0.56, 2 d.f.,P>.75). That there was no differential response before the addition of aphids indicates that predators, although present on plants before colonization occurred, quickly moved to fireweed with increased aphid densities.

D. Discussion

When selecting fireweed, both *M. valeriani* and *A. varians* responded only to variation in fireweed quality and plant exposure. There was no reaction, either positive or negative, to the presence of other aphids or ants. The initial distribution of aphids on fireweed plants was not simply random, but was determined by the aphids' choice of the largest fireweed shoots. Furthermore, spatial scales of host selection by *M. valeriani* and *A. varians* differed dramatically.

Other aphid species and insects respond to variation in their host plants (Kennedy et al. 1959, Cromartie 1975, Karieva 1983, Service 1984). In this study, there was an interaction between a plant's height, its exposure and its probability of being colonized. Small fireweed were colonized when in the open or away from large fireweed. As in other aphids, this pattern is consistent with host searching that is partially visual (Smith 1976a, Horn 1981, Service 1984). These other studies, however, have not demonstrated discrimination among host plants on larger scales.

Although both species feed on the fireweed inflorescence, how they perceive variation in their fireweed environment is not the same. *Macrosiphum valeriani* alates responded to fireweed on a greater spatial scale than did *A. varians*. Whereas *M. valeriani* alates selected large areas of exposed fireweed, and then settled on the largest shoots

within the areas, *A. varians* arrived in areas more or less at random, and then selected the tallest shoots found there. While *A. varians* discriminated only on the level of the individual fireweed shoot, *M. valeriani* alates chose larger fireweed shoots within areas of overall high quality.

Although apterous *M. valeriani* also colonized large fireweed, they colonized plants close to their winter host. These results agree with those from screenhouse experiments conducted in 1983, demonstrating that settlement by apterae is a function of the distance a shoot is from either a winter host plant or a fireweed shoot with a colony on it (see Chapter III).

This experimental study leads to the conclusion that the individual shoot is the "habitat" that *A. varians* selects, while an area of fireweed represents a habitat for *M. valeriani*. The inference that "habitat" differs between these aphids is supported by a study (Antolin in prep.) documenting movement by offspring of *M. valeriani* colonists to plants near the natal plant while still nymphs. *Macrosiphum valeriani* colonists choose a place to live not only for themselves, but for their dispersing offspring as well. This is not true for *A. varians*. Movement of offspring from a natal colony is almost exclusively by alates flying when they reach maturity, and movement from the natal colony to other fireweed is a considerable distance (more than a few meters, Antolin in prep.).

The role of competition

There is no evidence that competitive interactions between these aphid species has affected how they settle on fireweed. The lack of an inter- or intraspecific aphid effect in this experiment could be because densities high enough to decrease plant quality were not reached. In the fourth and fifth sampling periods, some fireweed in the marking treatment had up to 100 *M. valerianl* and up to 200 *A. varlans*. These densities may not have been sufficient to limit resources on colonized fireweed. Without resource depletion, avoidance of colonized shoots in favor of unoccupied fireweed of lower intrinsic quality would not be expected. The shift from selection of high quality colonized fireweed to lower quality unoccupied shoots would be expected only if the fitness of new arrivals on colonized plants dropped below the fitness attainable on empty fireweed (cf. Whitham 1980). Later in the season, when aphid colonies build up (>200 individuals), there could be a negative correlation between colonization and aphid density. The question remains whether large plants with large colonies are avoided by alate colonists in favor of smaller, lower quality plants that are empty. This question was not addressed directly because at high densities in the field, it is not possible to distinguish between newly settled alates and alates produced within the colony.

A partial solution to this question was found in 1983 screenhouse experiments (see Chapter III). *Macrosiphum*

valeriani apterae and alates did not settle differentially on potted fireweed plants with established colonies of either species. The plants in screenhouse experiments had enough aphids on them to decrease plant quality (up to 300 per plant), but there were no differences in colonization between occupied and unoccupied fireweed shoots. Screenhouse colonization experiments were not repeated on *A. varians* because alates would not settle onto plants when confined into a space as small as the screenhouse (2m by 2.4m by 1.6m), and because *A. varians* apterae did not move farther than the nearest fireweed plant, if at all.

Nonetheless, a pattern consistent with a competition hypothesis does exist on individual fireweed shoots. *M. valeriani* and *A. varians* feed on the lower part of the inflorescence, and at the very tip of the inflorescence, respectively, even in the absence of the other species (Addicott 1978b). This segregation may have occurred through competition for space or access to phloem on the inflorescence of a fireweed shoot. Considering that the aphids seldom co-colonize (see Table 4) and that the survival of individual colonies is low (Addicott 1978a), it is not likely that competition has a strong effect on the population dynamics of these aphids. It is more likely that segregation on individual shoots is because of differences in size and feeding ability of the aphids. *Aphis varians* is much smaller than *M. valeriani* at all instars, so that segregation on the inflorescence probably reflects

differences in size and length of the mouthparts (and therefore the ability to feed in the phloem), rather than some sort of competitive exclusion.

The roles of ants and predators

The roles of ants and predators in the population dynamics of aphids are closely related. Ants increase aphid population growth both by stimulating feeding and by protecting the aphids from their natural enemies (Way 1963, Addicott 1979). If ants influence settlement by either aphid species, there should have been differences between plots that had ants and those that did not. Ants were commonly observed on plants in removal plots with new aphid colonists, indicating that ants are capable of quickly finding aphids. In marking plots, fireweed shoots with *A. varians* colonies were almost always tended if there were ant nests nearby. That the aphids did not differentially respond to plots with ants in either treatment, even though ants regularly foraged on colonized fireweed in marking plots, indicates that ants had no effect on colonization.

Formica fusca and *Tapinoma sessile* were the most commonly observed ant species at Coal Creek. The lack of an ant effect could be because of the relatively weak interactions these two ant species have with *A. varians*, compared to other ant species found in the Rocky Mountains, (*F. cinerea*, for example, Addicott 1979). The result of no interaction between aphid settlement and ant foraging,

however, is further supported by the finding that *Formica cinerea* does not directly affect *M. valeriani* survival or reproduction (see Chapter III).

As in other aphid systems (Sanders and Knight 1968, Perrin 1976), predators and parasitoids are able of controlling the distributions of *M. valeriani* and *A. variana*. Predation and parasition are probably the greatest causes of the short survival (2-3 weeks) of most colonies of both aphid species (Addicott 1978a). In the case of *A. variana*, predators directly decrease population growth and survival of colonies. For *M. valeriani*, predators cause both direct and indirect mortality; some aphids are eaten, while others move off fireweed because of disturbance. In the 1981 colonization/predation experiment, only 2 *M. valeriani* artificially colonized onto fireweed shoots were subsequently found on other fireweed. Since fireweed around experimental plots had been cut down, the majority of *M. valeriani* dispersers probably perished before finding another host plant.

Predators were not common in the study areas during the 1982 colonization experiment. Well after the end of the experiment, however, during casual observations in the mid-August 1982, many more predators (mainly syrphid flies, bugs, mites, and lady beetles) were found associated with the aphid colonies. To evaluate the finding from the predation experiments, I will explore the finding that the predator-aphid interaction (where predator density changed with aphid density. Predator

54

densities were approximately equal at the start of both the 1982 and 1983 experiments. In both years, numbers of predators increased soon after aphids arrived in the areas.

The effects of pheromones

Because attacked aphids emit alarm pheromones (Nault and Phelan 1984), disturbance from predators and from the experimenter in the removal treatment may have altered aphid settlement. Plants that previously had aphids on them might have been avoided if the alarm pheromones had a long-lasting effect. Alarm pheromones, however, are effective only over short distances and only for short periods of time (Montgomery and Nault 1977, Calabrese and Sorenson 1978). This makes it unlikely that alarm pheromones induced aphids to avoid colonized fireweed shoots during the 1982 removal experiment, either on shoots within sampling plots or on nearby shoots. In any case, fireweed shoots that had aphids removed from them were recolonized more often than would be expected by chance (see Figures 4 and 5).

Aphids may have responded positively to aphid "odor" (Kay 1976). Kay found that *Aphis fabae* reacted to the presence of the odor of unalarmed aphids, but more significantly, found that the aphids' response to visual stimuli (a vertical black stripe) increased when aphid odor and the black stripe were presented together. Because predators play a strong a role in the population dynamics of these aphid species, aggregation to increase population

55

growth (Way and Cammell 1970) or to satiate predators (Kidd 1982) might be expected. Although no positive or negative aphid effects were found, that aggregation leads to increased population growth and survival remains a possibility. There could be an interaction between concentrated settlement on high quality plants and increased population growth because of grouped settlement (c.f. Way and Cammell 1970).

Conclusions

The differences in scale of search and selection by *M. valeriani* and *A. varians* can best be described as independent means of minimizing impacts of predators and parasitoids. Although the quality of host plants varies spatially, both species colonize plants that provide high population growth rates. The survival of colonies, even on the best host plants, is unpredictable because of the response of natural enemies. If predators and parasitoids cue onto the same habitat variables (i.e. shoot height) that the aphids use to choose host plants (Smith 1976b, Horn 1981), there is an increased risk associated with colonizing the largest plants.

The low survival of colonists and to the differences between aphid species in spatial scales settlement may be why inter- or intraspecific competition are not commonly observed in this system. First, because of low survival of colonists, conditions leading to competition between two

aphid clones of either species arise so infrequently that aphid-aphid avoidance is not expected. Second, because *M. valeriani* and *A. varians* discriminate among host plants on different spatial scales, colonizing aphids may never be at high enough densities within the same area for competitive interactions to occur (Kareiva 1982). For example, areas near rose bushes with large *M. valeriani* colonies may have high densities of *M. valeriani* colonists, but relatively few *A. varians* colonists, and even fewer successful *A. varians* colonies. With spatial heterogeneity of fireweed affecting discrimination by *M. valeriani* at larger scales than it does *A. varians*, areas with high densities of each species would inevitably differ. Even if competition on a single fireweed shoot is acute, it is localized to single shoots for short periods of time.

The patterns of settlement found in this study lead to the following scenario as an explaination of how the distributions of these aphids on their fireweed host come about. For *M. valeriani*, the biggest fireweed shoots, yielding the highest fecundity and growth rates, are colonized in an area with other suitable plants nearby. When predators arrive, the aphids disperse by walking onto surrounding plants. *Aphis varians* also chooses the largest plants in a given area, where faster growth rates will more quickly lead to the production of alates. If they happen to settle into an area that has large and active ant nests, this growth and survival of the colony will be enhanced even

57

further (Addicott 1979)). That way, some alate offspring will disperse to other areass with suitable fireweed before the colony is decimated.

Southwood (1977) pprovided a synthesis for examining habitats as "templates"' that determine the trade-offs between reproduction "heere and now" and "elsewhere and later". The template inocludes the variance of spatial and temporal favorableness (of habitats, and the isolation of habitats from each otheer. Developing optimal strategies for any species on that tesmplate depends upon the organism's life history (e.g. dorrmancy, polymorphism, reproductive characteristics) and diispersal ability. The alternative host selection strategies off *M. valeriani* and *A. varians*, linked to differences in life histories, are independent solutions to problems associated with reproduction and survival in a spatially and temporallly variable environment. The distributions of these co-occurring aphids are determined by differences in the aphiids' responses to their fireweed template.

E. Acknowledgements

Thanks go to I. Ccote, D. Duncan, D. Featherston, P. Marino, D. McKinnon, A..R. Palmer, S.G. Reebs, C. Scharf, M. Schroeder, J. Spence, ID. van Vuren, and S. Williams. I was ably assisted in the fiield by various Earthwatch volunteers, K. Jones, E. Michel andd especially K. Trostel. This study was supported by an NSIERC of Canada operating grant to

J.F.A. and a Sigma Xi Grant-in-aid of Research to M.F.A.

58

J.F.A. and a Sigma Xi Grant-in-aid of Research to M.F.A.

59

F. Literature cited

F. Literature cited

Addicott, J.F. 1978a. The population dynamics of aphids on fireweed: a comaprison of local populations and metapopulations. Can. J. Zool. 56: 2554-2564.

_____ 1978b. Niche relationships among species of aphids feeding on fireweed. Can. J. Zool. 56: 1837-1841.

_____ 1978c. Competition for mutualists: aphids and ants. Can. J. Zool. 56: 2093-2096.

_____ 1979. A multi-species aphid-ant association: density dependence and species specific effects. Can. J. Zool. 57: 558-569.

Annis, B., R.E. Berry, and G. Tamaki. 1982. Host preference of the green peach aphid *Myzus persicae* (Hemiptera: Aphididae). Environ. Entomol. 11: 824-827.

Bryant, E.H. 1969. A model of plant-to-plant movement by aphids: a new approach. Res. Pop. Ecol. 11: 34-39.

Calabrese, E.J. and A.J. Sorenson. 1978. Dispersal and recolonization by *Myzus persicae* following aphid alarm pheromone exposure. Ann. Ent. Soc. Amer. 71: 181-182.

Cody, M.L. 1981. Habitat selection in birds: the roles of vegetation structure, competitors, and productivity. Bioscience 31: 107-113.

Cromartie, W.J. 1975. The effect of stand size and vegetational background on the colonization of cruciferous plants by herbivorous insects. J. Appl. Ecol. 12:517-533.

Dixon, A.F.G. 1977. Aphid ecology: life cycles, polymorphism, and population regulation. Ann. Rev. Ecol. Syst. 8: 329-353.

van Emden, H.F. 1972. Aphids as phytochemists. Pp. 25-43 in

60

Harborne, J.B. (ed). Phytochemical ecology. Academic Press, London.

van Emden, H.F. and M.A. Bashford. 1969. A comparison of the reproduction of *Brevicoryne brassicae* and *Myzus persicae* in relation to soluable nitrogen concentration and leaf age (leaf position) in the brussels sprout plant. Ent. exp. apl. 12: 351-364.

Feinberg, S.E. 1975. The analysis of multidimensional contingency tables. Ecology 51: 419-433.

Gould, F. and R.E. Stinner. 1984. Insects in heterogeneous environments. Pp. 427-450 in Huffaker, C.B. and R.L. Rabb (eds). Ecological Entomology. Wiley Interscience, New York.

Griffiths, C.L. 1980. Effects of ant attendance on aphids. M.Sc. thesis, Univ. of Alberta.

Hagen, K.S., and R. van den Bosch. 1968. Impact of pathogens, parasites, and predators on aphids. Ann. Rev. Ent. 13: 325-413.

Hallett, J.G. 1982. Habitat selection and the community matrix of a desert small-mammal fauna. Ecology 63: 1400-1410.

Harrison, R.G. 1980. Dispersal polymorphisms in insects. Ann. Rev. Ecol. Syst. 11: 95-118.

Horn, D.J. 1981. Effect of weedy backgrounds on colonization of collards by green peach aphid, *Myzus persicae*, and its major predators. Environ. Entomol. 10: 285-289.

Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. Ecol. Monogr. 54: 187-211.

Karieva, P. 1982. Exclusion experiments and the competitive release of insects feeding on collards. Ecology 63: 696-704.

_____ 1983. Influence of vegetation texture on herbivore

61

populations: resource concentration and herbivore movement. Pp. 259-289 in Denno, R.F. and M.S. McClure (eds). Variable Plants and Herbivores in Natural and Managed Systems. Academic Press, New York.

Kay, R.H. 1976. Behavioral components of pheromonal aggegation in *Aphis fabae* Scopoli. Physiol. Entomol. 1: 249-254.

Kennedy, J.S. 1958. Physiological condition of the hostplant and susceptability to aphid attack. Ent. exp. appl. 1: 50-65.

_____ 1975. Insect dispersal. Pp 103-109 in Pimentel, D.(ed). Insects, Science, and Society. Academic Press, New York.

Kennedy, J.S., C.O. Booth, and W.J.S. Kershaw. 1959a. Host finding by aphids in the field. I. Gynoparae of *Myzus persicae*. Ann. exp. Biol. 47: 410-423.

Kennedy, J.S., and I.M.M. Fosbrooke. 1972. The plant in the life of the aphid. Pp. 129-140 in van Emden, H.F. (ed.). Plant/Insect Relationships. R.E.S. Symposium 6. John Wiley, New York.

Kidd, N.A.C. 1982. Predator avoudance as a result of aggregation in the Grey Pine Aphid, *Schizolachnus pineti*. J. Anim. Ecol. 51: 397-412.

Mattson, W.J. 1980. Herbivory in relation to plant nitrogen quality. Ann. Rev. Ecol. Syst. 11: 119-161.

Montgomery, M.E. and L.R. Nault. 1977. Comparative responses of aphids to the alarm pheremone, (E)-β-farnesene. Ent. exp. appl. 22: 236-242.

Muller, H.J. 1958. The behaviour of *Aphis fabae* in selecting its host plants, especially *Vicia fabae*. Ent. exp. appl. 1: 66-72.

Nault, L.R., and P.L. Phelan. 1984. Alarm pheromones and sociality in pre-social insects. Pp. 237-256 in Bell, W.J. and R.T. Carde (eds). Chemical Ecology of Insects.

62

Chapman and Hall, London.

Chapman and Hall, London.

Perrin, R.M. 1976. The population dynamics of the stinging nettle aphid, *Microlophium carnosum* (Buxt.). Ecol. Ent. 1:31-40.

Reitberg, B.D., J.H. Myers, and B.D. Fraser. 1979. The influence of predators on the movement of apterous pea aphids between plants. J. Anim. Ecol. 48: 111-122.

Sanders, C.J. and F.B. Knight. 1968. Natural regulation of the aphid *Pterocomma populifoliae* on bigtooth aspen in northern Lower Michigan. Ecology 49: 234-244.

Service, P. 1984. The distribution of of aphids in response to variation among individual host plants: *Uroleucon rudbeckiae* (Homoptera: Aphididae) and *Rudbeckia laciniata* (Asteraceae). Ecol. Ent. 9: 321-328.

Shiyomi, M. 1967. A model of plant-to-plant movement of aphids. I. Descriptions of the model. Res. Pop. Ecol. 9: 53-61.

Smith, J.G. 1976a. Influence of crop background on aphids and other phytophagous insects on Brussells sprouts. Ann. appl. Biol. 83: 1-13.

_____ 1976b. Influence of crop background on natural enemies of aphids on Brussells sprouts. Ann. appl. Biol. 83: 14-29.

Southwood, T.R.E. 1977. Habitat, the templet for ecological strategies? J. Anim. Ecol. 46: 337-365.

Walters, K.F.A. and A.F.G. Dixon. 1982. The effect of host quality and crowding on the settling and take-off of cereal aphids. Ann. appl. Biol. 101: 211-218.

Way, M.J. 1963. Mutualism between ants and honeydew-producing Homoptera. Ann. Rev. Ent. 8: 307-344.

Way, M.J. and M.E. Cammell. 1970. Aggregation behavior in relation to food utilization by aphids. Pp 229-247 in A.

63

Watson (ed). Animal Populations in Relation to Their Food Resources. R.E.S. Symposium 10. Blackwell Scientifc Publications, Oxford.

Watson (ed). Animal Populations in Relation to Their Food Resources. R.E.S. Symposium 10. Blackwell Scientifc Publications, Oxford.

Whitham, T.G. 1978. Habitat selection by *Pemphigus* aphids in response to resource limitation and competition. Ecology 59: 1042-1052.

_____ 1980. The theory of habitat selection: examined and extended using *Pemphigus* aphids. Amer. Nat. 115: 449-466.

Zucker, W.V. 1982. How aphids choose leaves: the roles of phenolics in host selection by a galling aphid. Ecology 63: 972-981.

III. The effects of aphiid density on the host selection and colony survival of *Macrosiphum valeriani* Clarke (Homoptera: Aphididae)

A. Introduction

Studies of habitatt selection and its effects on animal distributions have demonstrated (claimed) that animals choose places to live where they can find the most abundant and highest quality ressources (MacArthur and Levins 1964, Fretwell 1972, Rosenzweig 1973, Whitham 1978, 1980, Cody 1981, Hallet 1982). Haibitat quality depends upon not only the resources, but also on the number of potential competitors found within a habitat (Whitham 1978, 1980). Initial quality may decline as the number of colonists choosing the habitat increases. Those individuals arriving after the best habitats are settled may opt for habitats of intrinsically lower quality, where they will have greater fitness by avoiding competition for resources within the best habitats (Fretwell 1972, Whitham 1980).

The purpose of this study was to examine the effects of aphid densities on hostt plant selection and colony survival of the aphid, *Macrosiphum valeriani* Clarke. This aphid feeds on the inflorescence off its summer host, fireweed (*Epilobium (Chamerion) angustifollium* L.: Onagraceae). Specifically, experiments were carried out to determine whether *M. valeriani* avoids firewmed shoots with inter- or intraspecific competitors on them in favor of unoccupied

65

shoots. Further experiments were conducted to examine how *M. valeriani* is affected by high densities of the aphid *Aphis varians* (Koch), a potential competitor, that also feeds on fireweed inflorescences.

In a previous study of host selection by *M. valeriani* and *Aphis varians*, I demonstrated that both aphid species preferentially colonize tall fireweed within an area (see Chapter II). Addicott (unpubl. data) has demonstrated that tall fireweed shoots with large inflorescences provide better population growth for both species: tall fireweed shoots represent high quality habitats. Although at high densities these aphids compete for resources on a shoot (Addicott unpubl. data), no inter- or intraspecific aphid avoidance was found in the searching and settlement of either species (see Chapter II). Neither aphid species avoided shoots with aphids on them, regardless of the size of the fireweed shoot.

Those field colonization experiments were carried out at the beginning of the summer of 1982, when alates (winged morph) were flying onto fireweed from their winter hosts (*Rosa* spp. for *M. valeriani* and *Ribes* spp. for *A. varians*). The field study was carried out during the initial colonization of fireweed. Aphid populations were not dense enough during that experiment to deplete plant resources sufficiently to elicit an avoidance response by colonists of either aphid species. The experiments reported here were designed to examine whether *A. varians* and *M. valeriani*

residents affect host selection and survival of *M. valeriani* colonists. I used fireweed with larger aphid colonies than those seen during the 1982 field experiments (see Chapter II). The colonization study was carried out late in the summer of 1983 in a screenhouse using potted fireweed plants occupied by dense *M. valeriani* or *A. varians* populations.

A field experiment was carried out in late 1984 to determine the responses and population growth of *M. valeriani* apterae (non-winged morph) on fireweed shoots with large ant-tended *A. varians* colonies. Addicott (1979) has demonstrated that ants have a positive effect on the performance of *A. varians* populations, and suggested that *M. valeriani* is negatively affected by ants. The 1984 survival experiment examined the effects of both *A. varians* density and ant activity on *M. valeriani* population growth.

Aphis varians colonization was not studied in the screenhouse because alate behavior of this species was affected by the size of the screenhouse. Alates simply attatched themselves to the roof of the screenhouse until they starved. *Aphis varians* apterae moved only as far as the plant next to the release point (see Materials and Methods). Fireweed to fireweed dispersal by *A. varians* is almost exclusively by flying several meters away from the source shoot (Antolin in prep.). The screenhouse was not large enough to encompass the flight distance of dispersing alates.

B. Materials and methods

Colonization experiments

Five experiments were carried out in a 2.6m wide by 4.6m long by 2m high screenhouse at the Rocky Mountain Biological Laboratory at Gothic, Colorado (106°59' West, 39°57' North, el. 2886m) from August 24 to September 12, 1983. In an adjacent greenhouse of the same size, fireweed plants in 15 cm pots were grown from rootstock that had been dug up from natural stands of fireweed. Aphid stock colonies for use in experiments were maintained on potted plants in the same greenhouse. Every plant used for both stock colonies and experiments had an inflorescence. An experimental arena, constructed from a 120 cm² wooden pallet with uniformly spaced holes to accomodate 36 potted plants (six plants in each of six rows), was placed in the center of the screenhouse. In the arena, pots were 6.0 cm apart, and plants were on average 11.5 cm apart.

Three trials, A1 through A3, tested host selection by *M. valeriani* apterae. The trials were carried out consecutively. Three treatments were used within each trial: plants with either a *M. valeriani* colony (MAGNO treatment) or an *M. variana* colony (ADMIS treatment), or plants that were unoccupied (EMPTY treatment). In each trial, the 36 holes in the pallets were consecutively numbered, and a plant from one of the three treatments was randomly assigned to each place. Twelve plants were used in each treatment. The pallet

was bordered with green plastic lawn edging, and was filled with potting soil to cover the tops of the pots, providing a smooth obstacle-free surface in the arena. Two hundred apterous adults and fourth instar nymphs, marked with a colored powder, were released into the arena, and located two days later. To test for movement after initial settlement, apterae in Trial A3 were not removed from the fireweed they had colonized, but were left on the plants and located again two days later.

The aphids were released directly onto the soil surface of the arena, all at the same time. Trial A1 had two release points, with 100 aphids at each point; trials A2 and A3 had four release points, with 50 aphids released at each. There is no reason to believe that the powder adversely affected the aphids' movement, as no aphids died at the release point, and some even deposited nymphs on the fireweed in the arena. Aphids were considered settled if their stylets were inserted into the plants.

A fourth experiment using apterae, Trial A4, examined the settlement by apterae on fireweed with no aphids. Only unoccupied shoots were used in this experiment, but the procedure was otherwise identical to that in Trials A1-A3. Two hundred marked apterae were released into the arena at four points, and were located two days later.

Trial B, testing the host selection by alates, had only two treatments: plants with *A. varians* colonies (APHIS) and unoccupied plants (EMPTY). Eighteen plants from either

treatment were placed randomly in the pallet, and the arena was constructed as above. Plants with alate-producing stock colonies were introduced into the screenhouse, and experimental plants were censused two days later. Plants with *M. valeriani* colonies were not included because MACRO plants were producing alate adults by the time this experiment was carried out. It would not have been possible to distinguish between those alates that were produced within the colony and those that had arrived from other plants. The shift to alate production was probably in response to high aphid densities on the plants.

In trials A1 through A4, the distance from the release points to each plant was measured. In trials A2, A4 and B, plant height was measured as well. Plants chosen for use in trials A1 and A3 were of approximately the same height, to control for possible differences in plant quality. Plant height in trials A1 and A3 did not vary more than 20%.

In analyses of resident density only nonparametric tests were used because numbers of resident colonists on the experimental plants were not counted in every case, but were estimated and ranked for plants with high densities (more than 100 resident aphids). Measurements of distances from release points and plant measurements were both normal and homoscedastic, so parametric tests were used with those data.

Survival and reproduction experiments

During August 1984, experiments were carried out on a natural stand of fireweed at Spring Creek, Colorado (Gunnison National Forest, 106°46' West, 38°47' North, el. 2743m), to document interspecific effects on survival of apterous *M. valeriani*. This was study site SC22 used by Addicott (1978a, 1978c, 1979) in surveys of the ant-aphid-fireweed system. Up to 60 percent of all fireweed shoots at the site consistently have large *A. varians* colonies on them. The area has a history of large and healthy ant nests (*Formica cinerea*) tending *A. varians* colonies, and few *M. valeriani* colonies (Addicott, personal observation).

A two-way factorial experiment was run twice, Trial 1 from August 11 to August 18, and Trial 2 from August 23 to September 4. The two main effects were shoots with natural colonies of *A. varians* present or absent, and ants excluded or not. The same group of fireweed was used in both trials, but those shoots that had ants foraging on them during Trial 1 had ants excluded from them during Trial 2, and vice versa.

Three days prior to the beginning of each trial, all fireweed shoots were barriered with tanglefoot to exclude ants. The following day adult apterous *M. valeriani*, collected from nearby sites, were put into net bags that were placed over the inflorescence of the experimental shoots. Aphids were marked with a colored powder. In Trial

1, 5 apterae were placed on each fireweed shoot; 6 apterae per shoot were used in Trial 2. The aphids were allowed to settle on the fireweed for 2 days, when all bags were removed, and tanglefoot barriers were taken off shoots in the accessible-to-ants treatments. The experiments were monitored every day for at least five days, Trial 2 was censused once more 10 days after the removal of the barriers. The numbers of remaining adults and the numbers of *Macrosiphum valeriani* offspring were counted at each census; predators and other insects were noted if present, but were not removed. At the end of each trial, the size of *A. varians* colonies was estimated using the method of Addicott (1978a), and shoot height was measured.

Aphid survival and reproduction data were normally distributed when log transformed. This experiment was analyzed using a two-way analysis of variance with covariance, using shoot height as the covariate to control for possible differences in plant quality among treatments.

C. Results

Colonization

In screenhouse colonization trials, *M. valeriani* apterae did not colonize fireweed without aphids (the EMPTY treatment) more often than plants with aphids (APHIS and MACRO treatments; Table 6). The median numbers of apterae settling on plants were not different among treatments

Table 6 -- Comparison of numbers of plants colonized among treatments. Trials A1-A3 tested selection by *M. valeriani* apterae, Trial B tested alate selection. 200 apterae were released in trials A1-A3. 2 d.f. in all analyses, except Trial B, 1 d.f.

	Date	# aphids recovered	# of fireweed colonized APHIS	MACRO	EMPTY	χ^2	P
Trial A1	Aug 26	131	9	6	10	3.40	.19
Trial A2	Aug 28	151	9	12	8	3.56	.17
Trial A3	Sept 1	107	9	9	10	0.32	.85
	Sept 3	91	10	9	11	1.20	.55
Trial B	Sept 12	41	9	----	13	1.87	.17

(Table 7). Furthermore, settlement by *M. valeriani* apterae was not correlated with density of *M. valeriani* or *A. varians* colonies (Table 8).

In Trial A3 the numbers of apterae found on fireweed changed in the time between the first count on September 1 and the second count on September 3 (Table 6). Only 91 marked apterae were found during the second count, 20 on EMPTY plants, 26 on APHIS plants, and 45 on MACRO plants. This difference was significant; most apterae moved from EMPTY plants onto plants with aphid colonies on them (Table 7). At the first census of Trial A3, 33 apterae were found on EMPTY plants, 19 on APHIS plants, and 34 on MACRO plants.

The low numbers of marked aphids recovered in Trial A3 resulted from many of the 4th instar nymphs used in this trial losing their marks when they molted to the adult stage. Many unmarked adult aphids were found on EMPTY and APHIS plants. At the first count on September 1, 13 unmarked *M. valeriani* were found on 6 EMPTY plants, and 16 unmarked aphids were found on 7 APHIS plants. On September 3, 21 unmarked apterae were found on 9 EMPTY plants, and 17 unmarked apterae were found on 8 APHIS plants. These aphids were not included in the analyses. Including them would have biased the results because unmarked *M. valeriani* adults on MACRO plants could not be separated into those that had been raised on the experimental plants and those that had been released into the arena. If one assumes that an equal proportion of 4th instars molted and lost their marks on

Table 7 -- Median number of *M. valeriani* found on colonized plants. Trials A1-A3 tested colonization by apterae, Trial B tested alate colonization. 2 d.f. in all analyses, except Trial B, 1 d.f.

	Date	median # of *M. valeriani* on colonized fireweed APHIS	MACRO	EMPTY	Kruskal Wallis H	P
Trial A1	Aug 26	3	4	2	0.45	.80
Trial A2	Aug 28	5	3	2	0.96	.62
Trial A3	Sept 1	2	3	2	3.12	.20
	Sept 3	2	5	2	6.01	.049
Trial B	Sept 12	1	----	2	.540	.46

Table 8 -- Rank correlation coefficients of number of *M. valeriani* colonists with resident density (ranges of densities in parentheses).

	N	Correlation with resident density	
		M. valeriani	*A. varians*
Trial A1	12	0.015 (8-100)	0.313 (4-100)
Trial A2	12	-.014 (20-85)	-.481 (5-200)
Trial A3	12	0.089 (27-175)	-.469 (15-100)
	12	0.115 (45-190)	-.341 (0-175)
Trial B	18	----	0.077 (5-350)

plants in all three treatments, the results are not affected, and 70% of the aphids released into the arena can be accounted for.

The only consistently significant relationship found in these colonization trials was between the number of apterae colonizing a plant and the plant's distance from the release points (Table 9). Apterae moved onto plants nearest the point where they were released. To test whether the presence of aphids on plants in trials A1-A3 affected the distance that apterae moved, the slopes of the regressions between number of aphids colonizing and average distance from release points in trials A1-A3 were compared to the slope of the relationship in Trial A4. One would expect a steeper negative slope in Trial A4, where all plants were unoccupied, if *M. valerinai* apterae moved farther in treatments where aphids were present. The slopes did not differ among trials ($F=0.54$, 3,136 d.f., $P=.65$), indicating that dispersal distance was not affected by the presence of aphids on plants.

Apterae did not respond to differences in plant height within the arenas. In trails A2 and A4, where plants from a wide range of heights were used, the correlation between number of colonizing apterae and plant height was not significant (A2, $r=-.165$;A4, $r=.169$). Height varied from 67.5 cm to 117.8 cm in Trial A2, and was not different among the three treatments ($F=.841$, 2,33 d.f., $P>.44$). In Trial A4, height varied from 65.8 cm to 116.5 cm. Because plant

Table 9 -- Slopes and r' values of the regression between log (x+1) number of colonizing *M. valeriani* apterae and average distance from the release points. ** P<.001, N=36. Slopes did not differ among trials.

	slope	r'
Trial A1	-.022	.38 **
Trial A2	-.020	.35 **
Trial A3	-.016	.41 **
Trial A4	-.023	.54 **

height did not vary more than 20% within trials A1 and A3, it is doubtful that plant height affected colonization in those trials either.

Host selection by alate *M. valeriani* during Trial B was similar to host selection in previous field experiments (see Chapter II). Alates did not respond to the presence (Table 6) or density (Table 7) of *A. varians*. There was a significant correlation, however, between numbers of alates colonizing and plant height (Figure 11; r=.467, N=36, P<.01). An analysis of covariance was carried out to test the null hypothesis that *M. valeriani*'s reaction to plant height was not affected by *A. varians*. EMPTY plants were larger ($\bar{x}$=87.3 cm, range 71.9 to 111.2 cm) than APHIS plants ($\bar{x}$=80.1 cm, range 61.6 to 91.6 cm), but the difference was not statistically significant (t=1.89, 34 d.f.,P>.06). Analysis of covariance controlled for the differences in height between treatments. Slopes of the relationship between settlement and plant height were parallel (F=1.57, 1,32 d.f., P=.22), and the intercepts of the lines coincided (F=.98, 1,33 d.f., P=.33). The null hypothesis was not rejected; adjusted means of numbers of colonizations did not differ bewteen the EMPTY ($\bar{x}$=1.34) and APHIS ($\bar{x}$=.94) treatments. In no case in this study, or in previous work (see Chapter II), did the presence of *Aphis varians* alter the host plant selection of *Macrosiphum valeriani*.

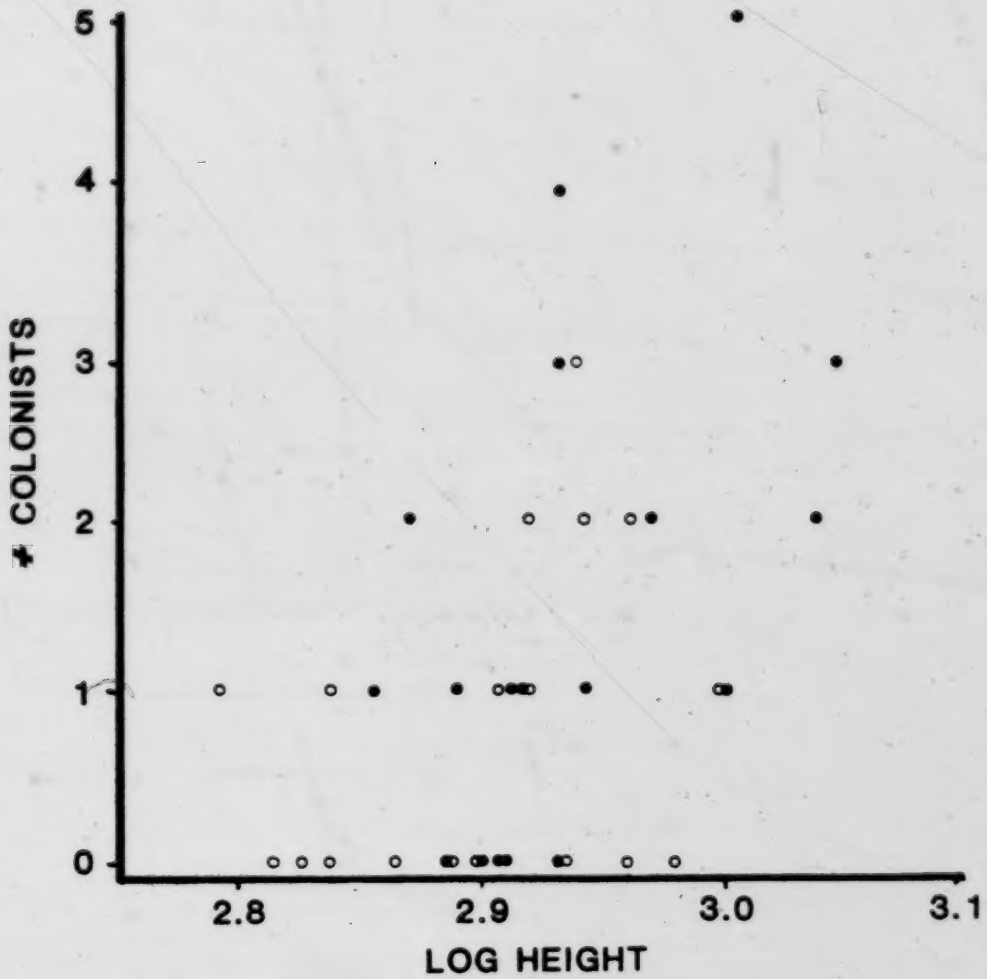


Figure 11. Relationship between colonization by alates and plant height in Trial B. • are empty plants, o are plants with *A. varians* colonies.

Survival and reproduction

In survivorship trials at Spring Creek, the presence of *A. varians* had a strong effect on how long *M. valeriani* apterae remained on the fireweed. Analysis of variance with covariance, including the two main effects (aphids and ants) and the covariate (fireweed shoot height), was calculated separately for each day of the experiment. The decrease in numbers of *M. valeriani* apterae was significantly greater on *A. varians* shoots in both Trial 1 and Trial 2 (Table 10), but the numbers remaining did not change greatly after the second day. Ant foraging did not consistently affect the behavior or survival of *M. valeriani* apterae in either trial. There was a significant ant effect only on the fourth and fifth days of the second trial, and interaction terms were never significant. The covariate, fireweed shoot height, did not alter the significance of the aphid effect. Plant height influenced the result from the two-way ANOVAs only on Day 0 of the second trial. There was only a 16% difference among mean height in the four treatment groups in Trial 1, and 12% variation among means in Trial 2 (Table 11).

A significant negative relationship was found between *A. varians* density and the numbers of *M. valeriani* remaining on the fireweed on the last day of each experiment (Figure 12). The fates of most *M. valeriani* apterae during these experiments is unknown (Table 11), the majority were not found again on either experimental or surrounding fireweed

Table 12 — Mean number of *H. calceiformis* adults found in the survival experiments, 0 DAT, 30 DAT, 1 YR & 2 YRS in Trial 1, 1.33 g.c. in Trial 2. * indicates that the corrected mean height had a significant effect.

Trial 1

# of Insects	no spider no wire	no spider wire	spider no wire	spider wire	[illegible] spider	[illegible] spider
	0	6	7	8		
Day 0	6.00	6.00	6.00	6.00	0.00	0.00
Day 1	5.00	5.83	4.86	5.00	0.00	0.00
Day 2	5.00	5.17	5.86	4.17	0.0100	0.00
Day 3	5.00	5.00	4.14	4.00	0.0000	0.00
Day 6	5.00	5.17	4.14	5.00	0.0100	0.00
Day 9	5.00	5.00	5.00*	5.00	0.0100	0.00*
Day 6	5.00	5.00	5.00*	5.00	0.0000	0.00*

Trial 2

# of Insects	no spider no wire	no spider wire	spider no wire	spider wire	[illegible] spider	[illegible] spider
	4	5	6	7		
Day 00	6.00*	6.00	6.00	6.00	0.00	0.00
Day 1	5.00	5.00*	5.00	5.00*	0.0000	0.00
Day 3	5.00	5.00	4.70	4.00	0.0000	0.00
Day 9	5.00	5.00	4.00	5.00	0.0000	0.00
Day 6	5.00*	5.00	4.00	5.00	0.0000	0.00
Day 9	5.00*	5.00	4.00	5.00	0.0000	0.00
Day 00	4.00	5.00	5.00	5.00	0.00	0.00

Table 11 -- Number of shoots, average shoot height (cm), and fates of adult *M. valeriani* in the Spring Creek survival experiment.

Trial 1	no aphids no ants	no aphids ants	aphids no ants	aphids ants
# shoots	5	6	7	6
ave. hgt.	104.9	92.9	92.9	87.3
% missing	32	40	89	87
% found dead	4	7	3	7
% moved from another shoot	4	13	9	7

Trial 2	no aphids no ants	no aphids ants	aphids no ants	aphids ants
# shoots	6	6	8	8
ave. hgt.	92.1	98.9	88.1	100.6
% missing	50	58	58	79
% found dead	6	12	13	4
% moved from another shoot	14	3	4	0

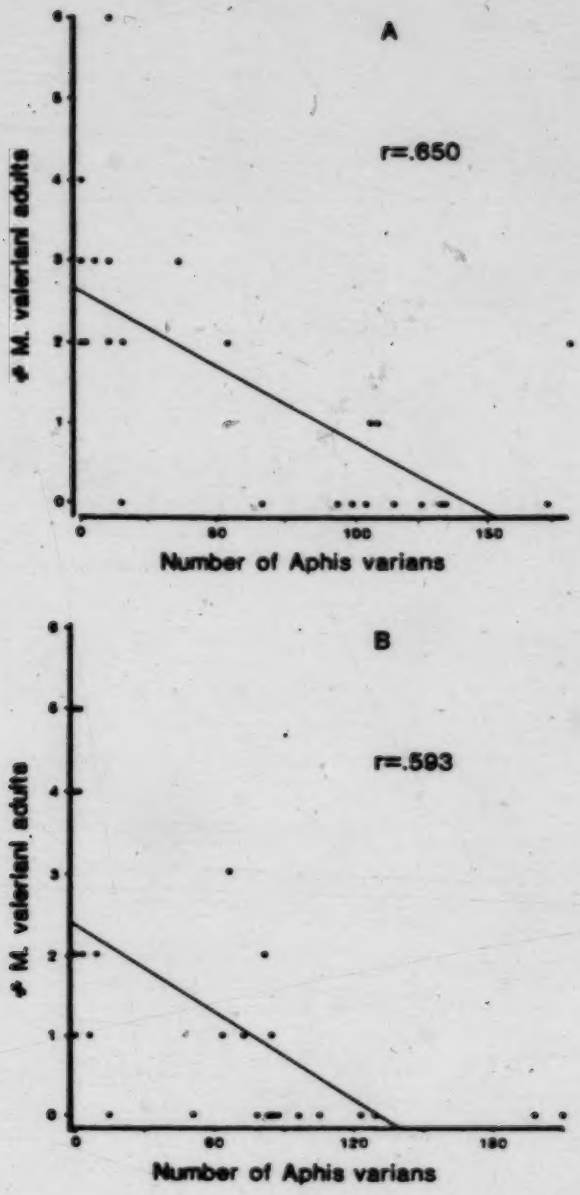


Figure 12. Relationship between number of *Macrosiphum valeriani* remaining on a fireweed shoot and the size of the *Aphis varians* colony on the shoot, at the end of 1984 Spring Creek experiments. A.) Trial 1, relationship on Day 6. B.) Trial 2, relationship on Day 5.

shoots. Few of those apterae lost during the experiments were killed by predators, although predators were commonly seen foraging on fireweed with *A. varians* colonies, and sometimes on empty shoots. Some apterae on plants with large *A. varians* colonies may have starved, as whole bodies that had no visible predator damage were found. Apparently, most apterae walked off the fireweed shoots, although almost none were subsequently found on other fireweed.

The reproductive rate of *M. valeriani* was greatly reduced on fireweed with *A. varians* colonies (Table 12). This rate is defined as the number of nymphs on a shoot at a given census, divided by the total number of adult-days that apterae had remained on the plant up to that census. Reproductive rate was generally twice as great in Trial 1 as in Trial 2, but in both cases reproductive rate became constant after the third day. The size of the developing colony on the last sampling day was inversely related to the density of *A. varians* (Figure 13).

Again, neither the presence of ants nor fireweed shoot height consistently affected the outcome. Both were significant for Day 1 in the first trial; fireweed with with ants foraging on them had lower population growth on Day 5 of the second trial (Table 12).

Table 12 -- *M. valeriani* reproduction in the survival experiments (mean number of nymphs per adult-day). Day 0 is when bags and barriers removed from fireweed, 2 days after adult aphids first placed on fireweed. * P<.05, ** P<.01, 1,19 d.f. in Trial 1, 1,23 d.f. in Trial 2. † indicates that the covariate, shoot height, had a significant effect.

Trial 1

	no aphids no ants	no aphids ants	aphids no ants	aphids ants	F-ratio Aphid Effect	F-ratio Ant Effect
Day 1†	0.19	0.26	0.23	0.30	5.18 *	9.64 *
Day 2	1.07	1.06	0.38	0.28	24.34**	0.02
Day 3	1.42	1.41	0.37	0.67	27.27**	0.60
Day 4	1.39	1.71	0.41	0.20	47.98**	0.11
Day 5	1.31	1.49	0.26	0.23	42.26**	0.00
Day 6	1.39	1.74	0.28	0.27	36.29**	0.24

Trial 2

	no aphids no ants	no aphids ants	aphids no ants	aphids ants	F-ratio Aphid Effect	F-ratio Ant Effect
Day 0	0.23	0.21	0.11	0.12	8.22**	0.15
Day 1	0.51	0.52	0.25	0.08	12.63**	2.29
Day 2	0.48	0.38	0.18	0.24	4.68 *	0.01
Day 3	0.59	0.54	0.14	0.10	31.78**	1.13
Day 4	0.70	0.57	0.17	0.08	38.94**	3.49
Day 5	0.70	0.55	0.28	0.08	27.73**	6.42 *
Day 10	0.61	0.41	0.21	0.09	12.22**	2.43

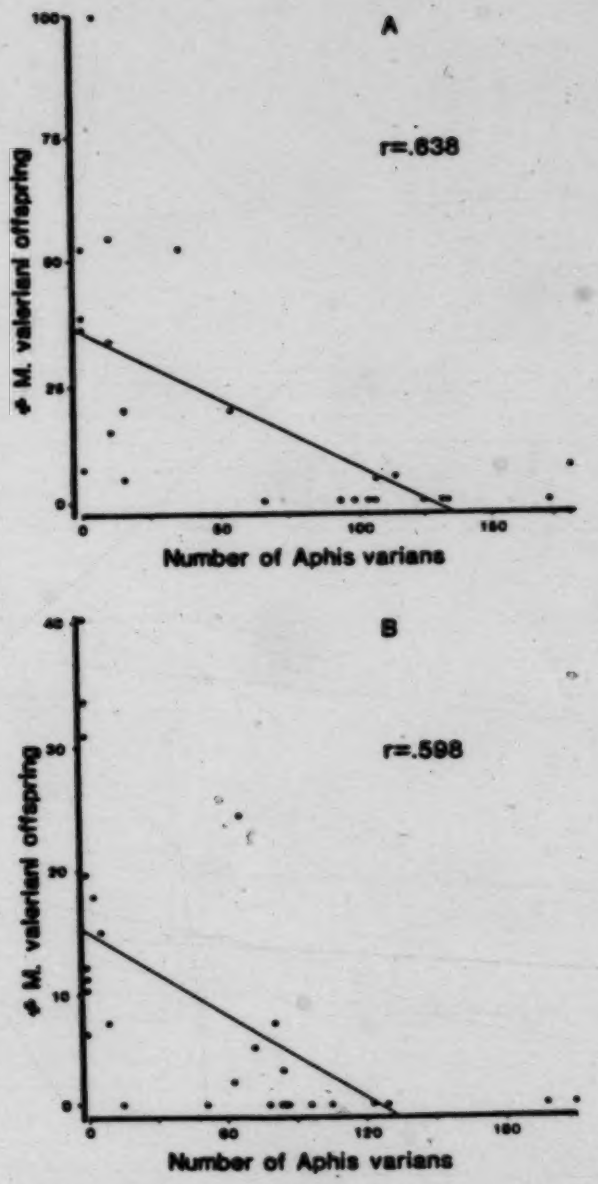


Figure 13. Correlation of the size of the developing *Macrosiphum valeriani* colony and the size of resident *Aphis varians* colony at the end of 1984 Spring Creek experiments. A.) Trial 1, relationship on Day 6. B.) Trial 2, relationship on Day 5.

D. Discussion

Contrary to the finding in the screenhouse experiments that host selection was not influenced by density of resident aphids, there was a strong interspecific effect by *A. varians* on both the movement and reproduction of *M. valeriani* apterae in Spring Creek experiments. At Spring Creek, the probability of an *M. valeriani* aptera staying on a host plant and the growth rates of *M. valeriani* populations were both inversely related to size of the resident *A. varians* colony. In the screenhouse, there was no preference for EMPTY fireweed shoots over occupied fireweed. Additionally, in Trial A3, where apterae were left in the experimental arena for 4 days, no movement away from occupied plants was observed.

There are two plausible, but not mutually exclusive, hypotheses that may explain the discrepancy between the screenhouse colonization trials and field survivorship trials. First, host plant quality of screenhouse plants may have been greater than the quality of natural fireweed shoots at Spring Creek. Unless resources were limited on APHIS and MACRO plants in the screenhouse, there is no reason to expect avoidance of those fireweed. Second, the activities of predators and other insects associated with large *A. varians* colonies may have interfered with the settlement of apterae on APHIS plants at Spring Creek. All insects other than aphids were kept out of the screenhouse, so the same type of interference could not have occurred

during colonization trials.

Fireweed quality

Because host plant quality affects Homopteran herbivores in a variety of ways (Whitham 1978, Zucker 1982, Denno 1983, Karieva 1983), differences between the quality of potted fireweed plants and fireweed shoots used in the field may account for some of the disparities found in these two sets of experiments. Average heights were similar for laboratory and field plants, but there may have been differences in levels of soluble nitrogen between potted and natural fireweed. Potted plants were fertilized regularly at two week intervals until the beginning of the screenhouse experiments.

Host plant quality also may change with resident herbivore density (Whitham 1978, 1980). Although there were similar sized *A. varians* populations on screenhouse plants and Spring Creek shoots (compare aphid density ranges in Table 8 with those in Figure 12), it is possible that resources on potted plants with resident aphid colonies in screenhouse experiments were not altered sufficiently to lower plant quality. Without differences in quality between occupied and empty plants, *M. valeriani* alates and apterae would not be expected to favor empty plants.

Two other factors lead to the conclusion that fireweed shoot quality at Spring Creek was lower than quality of potted fireweed plants. Most *A. varians* populations were

declining at Spring Creek, because of dispersal from fireweed by *A. varians* alates and because of the activities of predators. Before the beginning of the survivorship trials, some *A. varians* colonies were undoubtedly much larger (up to 1000 aphids) than during and after the experiments. Plants with *A. varians* colonies on them had probably been sapped of some resources.

Aphid feeding causes a stunting of the inflorescence. The inflorescence of Spring Creek plants comprised only about 20% of total height; potted plants had inflorescences that averaged 30% of total height. If the relative size of the inflorescence is determined by the amount of resources a plant has for reproduction or the degree of stunting because of aphid feeding, inflorecence length would reflect plant quality. This would be true especially for these aphids that both feed on the inflorescence.

Although, these were not direct measures of plant quality, they are suggestive of differences in resource levels between the two groups of plants. Fewer resources on fireweed shoots at Spring Creek may have caused lowered *M. valeriani* reproduction on plants with *A. varians* colonies, because of exploitative competition between the two aphid species.

Interference by other insects

In Spring Creek experiments, movement of *M. valeriani* apterae from plants with *A. varians* colonies may have been a

response to low resource levels, but it may have been a reaction to interference by insects other than aphids as well. Aphids in tribe Macrosiphini, of which *M. valeriani* is a member, respond strongly to aphid alarm pheromones either by walking or dropping from the plant where they are disturbed (Nault, Montgomery, and Bowers 1976, Montgomery and Nault 1977). Alarmed aphids generally do not return to the plant they left (Montgomery and Nault 1977). It is possible that this occurred during Spring Creek experiments, as the majority of *M. valeriani* did not return to the same plant once they had left. Similar results were found in an aphid addition experiment carried out in 1983 (see Chapter II).

Disturbance by predators, flies (probably Muscidae), and plant-feeding mirid bugs may have induced the *M. valeriani* apterae at Spring Creek to disperse. In Spring Creek Trial 2, where predators were more carefully recorded than in Trial 1, predators (spiders, syrphid larvae, hymenopterous parasitoids, coccinellid larvae, anthocorids, halictid bees, staphylinid beetles, mites) were noted at 40 of the 112 (36.1%) observations of plants with *A. varians* colonies, and only at 8 of 84 (9.5%) observations of unoccupied plants. Mirid bugs were observed an equal percentage of times on both occupied and unoccupied fireweed (≈25% of observations). Flies were not counted, but they were almost always associated with large *A. varians* colonies, often feeding directly on the honeydew being

secreted by the aphids.

Ants were thought to cause both dispersal and mortality of *M. valeriani* (Addicott 1979). Addicott found a negative correlation between ant activity and the presence of *M. valeriani* at Spring Creek, and concluded that ants must have a direct effect on *M. valeriani*. Because his sampling period (weekly) was longer than the daily samples taken during this Spring Creek experiment, he was not able to discern between competitive aphid effects or impacts of predators and other insects, and the direct effects of ants.

Ants react to and remove alarmed aphids from fireweed. Aphids placed onto tended *A. varians* colonies with a camel-hair brush were quickly removed by ants if they moved rapidly among the colony, but were left untouched if they did not move. This interaction between ants, alarm pheromones, and movement has been demonstrated in other aphid-ant systems (Nault, Montgomery and Bowers 1976). If predators, flies or mirids alarmed *M. valeriani* during the Spring Creek experiment, some of the missing aphids may have fallen prey to ants, either on the plant or on the ground after they had dropped from the fireweed shoots. Since ant effects were not consistently found in the analysis of the Spring Creek data, and statistical interactions between ant effects and aphid effects were never seen (Table 5), the interactions between alarm pheromones and ant activities were not of great importance during the Spring Creek experiments.

Comparison of apterae and alates

Macrosiphum valeriani alates and apterae exhibit different preferences when choosing a place to live. Alates select and settle on the tallest fireweed in an area (also see Chapter II), while apterae colonize fireweed shoots near the point from which they begin their dispersal movement. Although it has been demonstrated that there is potentially strong interspecific competition between *M. valeriani* and *Aphis varians*, neither the alates nor the apterae of *M. valeriani* preferred to settle on empty plants over those already occupied by *A. varians*. Additionally, in the experiments carried out in the screenhouse, apterae colonizers responded to neither intraspecfic densities nor to plant quality.

These experimental colonization results echo the conclusions from field observations of *M. valeriani* (see Chapter II). *Macrosiphum valeriani* gain greater fitness on taller plants (Addicott unpubl. data). In addition, *M. valeriani* alates select areas of high quality shoots, where there are high quality shoots not only for themselves, but for their apterous offspring as well (see Chapter II). When *M. valeriani* colonies are disturbed, usually by predators, apterae disperse to surrounding plants (Antolin in prep.).

Movement by dispersing apterae to the nearest fireweed shoots can best be explained in light of two costs associated with dispersal by walking: the risk associated with finding another host (Whitham 1978, Roitberg et al.

1979) and reduced reproduction after an interruption in feeding (Ward and Dixon 1982). Aphids moving off hosts in both the survivorship trials reported here, and in an addition experiment carried out in 1983 (see Chapter II) were seldom found on fireweed shoots in experimental plots again. It is doubtful that these dispersing aphids found another fireweed shoot, because in both experiments, experimental fireweed were isolated from other stands of fireweed. The majority probably fell victim to ground predators and foraging ants. Furthermore, it has been demonstrated that starved aphids resorb embryos (Ward and Dixon 1982), and that aphids have lower fecundity on the days after dispersal than at other times (Roitberg et al. 1979). The trade-offs between dispersal distance, lowered reproduction and the risk of predation during dispersal would have to be studied experimentally in *M. valeriani*. Movement and colonization by apterae, however, fits a pattern consistent with a cost of movement hypothesis.

Conclusions

Macrosiphum valeriani is seldom observed on fireweed with high densities of *A. varians*. Using the data presented here and evidence from another study of aphid host selection (see Chapter II), it is possible to tease apart the relative importance of host choice, exploitative competition and interference in controlling *M. valeriani* distributions. I hypothesize that although competition occurs between *M.*

valeriani and *A. varians*, it seldom arises because of the host selection and dispersal by *M. valeriani*.

But first, a brief summary of the evidence: 1) In screenhouse experiments, where there were no insect species other than aphids present, settlement and subsequent movement were not influenced by the presence of other aphids; 2) in field colonization experiments carried out in 1982, ants, aphids and predators were present, yet there were no aphid effects on colonization (see Chapter II); 3) at Spring Creek, where both aphid densities and predator densities were higher than in previous experiments, *M. valeriani* was affected by *A. varians*, both directly, via exploitative competition, and indirectly because of disturbance by other insects that were associated with large *A. varians* colonies; 4) there were healthy *M. valeriani* colonies 20m from the Spring Creek experiment site indicating that *M. valeriani* could have colonized the area, but was excluded.

These sympatric, potentially competing species are seldom found on the same host plant because of the response of *M. valeriani* to conditions on a host plant after settlement. Host plant quality changes because of the build-up of competitors, but mainly by interference from predators. *M. valeriani* alates choose plants on the basis of quality whether *A. varians* is present or not (see Chapter II). Although competition for resources is possible, it is rare because predators, parasitoids, and weather lower the

survival of colonists and colonies (Addicott 1978a, see Chapter II). *Macrosiphum valeriani* on plants with enough other aphids present to deplete resources still have the option of moving to nearby plants, where a better situation may exist. Since movement by apterae is to the nearest, yet not necessarily the best, fireweed, and since there is a cost associated with movement, the "adaptedness" of movement after colonization becomes clouded.

These results point to a number of inadequacies of habitat selection studies in making the link between initial choices and subsequent distributions. The majority of habitat selection studies conclude that habitat suitability is determined mainly by resource levels, and that resource levels change predictably with the density of residents within a habitat (Fretwell 1972, Whitham 1978,1980, Cody 1981). Animals are expected to optimize their habitat selection, and choose those habitats that are the most suitable through time. Yet the link between habitat selection and the expected survival and reproduction within habitats may not be as strong as habitat selection models assume. Habitat selection and subsequent survival may be separate and different processes. If habitats are unpredictable in time, there can be no optimization based upon long-term suitability and competitors. There can only be selection of habitats that will provide the fastest growth rates in the immediate future, so that good places to live and reproduce can be taken greatest advantage of for as

long as they remain suitable (cf. Southwood 1977). If reproduction is successful "here and now", then progeny can disperse to other habitats that are suitable "elsewhere and later" (Southwood 1977, Denno 1983).

E. Acknowlegements

The field work and preparation of this study would not have been as enjoyable without the complicity of I. Cote, H. Cushman, L. Dorn, P. Marino, A.R. Palmer, K. Shaw, J.R. Spence, D. van Vuren, and S. Williams. My time in Colorado was supported by an NSERC of Canada operating grant to John Addicott.

F. Literature cited

Addicott, J.F. 1978. The population dynamics of aphids on fireweed: a comaprison of local populations and metapopulations. Can. J. Zool. 56: 2554-2564.

_____ 1979. A multi-species aphid-ant association: density dependence and species specific effects. Can. J. Zool. 57: 558-569.

Cody, M.L. 1981. Habitat selection in birds: the roles of vegetation structure, competitors and productivity. Bioscience 31: 107-113.

Denno, R.F. 1983. Tracking variable hosts in space and time. Pp. 291-335 in Denno, R.F. and M.S. McClure (eds). Variable Plants and Herbivores in Natural and Managed Systems. Academic Press, New York.

Fretwell, S.D. 1972. Populations in a Seasonal Environment. Princeton University Press. Princeton, New Jersey. 217pp.

Hallet, J.G. 1982. Habitat selection and the community matrix of a desert small-rodent fauna. Ecology 63: 1400-1410.

Karieva, P. 1983. Influence of vegetation texture on herbivore populations: resource concentration and herbivore movement. Pp. 259-289 in Denno, R.F. and M.S. McClure (eds). Variable Plants and Herbivores in Natural and Managed Systems. Academic Press, New York.

MacArthur, R.H. and R. Levins. 1964. Competition, habitat selection, and character displacement in a patchy environment. Proc. Nat. Acad. Sci. 51: 1207-1210.

Montgomery, M.E. and L.R. Nault. 1977. Comparative responses of aphids to the alarm pheremone, (E)-*B*-farnesene. Ent. exp. appl. 22: 236-242.

Nault, L.R., M.E. Montgomery, and W.S. Bowers. 1976.

Ant-aphid association: roles of aphid alarm pheromone. Science 192: 1349-1351.

Roitberg, B.D., J.H. Myers, and B.D. Frazer. 1979. The influence of predators on the movement of apterous pea aphids between plants. J. Anim. Ecol. 48: 111-122.

Rosenzweig, M.L. 1973. Habitat selection experiments with a pair of co-existing heteromyid rodents. Ecology 54: 111-118.

Southwood, T.R.E. 1977. Habitat, the template for ecological strategies? J. of Anim. Ecol. 46: 337-365.

Ward, S.A. and A.F.G. Dixon. 1982. Selective resorption of aphid embryos and habitat changes relative to life-span. J. of Anim. Ecol. 51: 859-864.

Whitham, T.G. 1978. Habitat selection by *Pemphigus* aphids in response to resource limitation and competition. Ecology 59: 1042-1052.

_____ 1980. The theory of habitat selection: examined and extended using *Pemphigus* aphids. Amer. Nat. 115: 449-466.

Zucker, W.V. 1982. How aphids choose leaves: the roles of phenolics in host selection by a galling aphid. Ecology 63: 972-981.